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A TAXONOMIC REVISION OF
CARIBBEAN *ADIANTOPSIS*
(PTERIDACEAE)^{1,2}

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ABSTRACT

Adiantopsis Fée (Pteridaceae) is a relatively unstudied tropical cheilanthoid fern genus. In the present work, we evaluated the taxonomy and relationships among Caribbean *Adiantopsis* by examining 136 characters from approximately 500 herbarium specimens. This study identified nine Caribbean *Adiantopsis* species, three of which are newly described (*A. parvisegmenta*, *A. pentagona*, and *A. vincentii*). Additionally, an intriguing pattern of morphological and reticulate evolution was revealed by the analyses. *Adiantopsis* consists of three different laminar morphologies; palmate, pedate, and pinnate. The two pedate taxa are hypothesized to be fertile allotetraploid derivatives of the palmate *A. radiata* (L.) Fée and two different pinnate taxa. In this regard they parallel the origin of the South American *A. ×australopedata* Hickey, M. S. Barker & Ponce. Based on our analyses, it appears that pedate laminar morphologies in *Adiantopsis* independently originated multiple times via hybridization. This study provides testable hypotheses of morphological and reticulate evolution in the genus and presents a novel view of Caribbean *Adiantopsis*.

Key words: *Adiantopsis*, Caribbean flora, cheilanthoid, ferns, monilophytes, Pteridophytes.

Adiantopsis Fée is a cheilanthoid fern genus found throughout tropical America (Tryon & Tryon, 1982) and possibly Africa (Moran & Smith, 2001). A combination of echinate spores, distinct pseudoindusia, adaxial carinae, and unique septate-capitate hairs on the axes and laminar surfaces distinguishes *Adiantopsis* from other cheilanthoids. Historically, the genus was interpreted to include seven species,

four of which occur in the Caribbean, predominantly in Cuba and Jamaica (Tryon & Tryon, 1982). In this regional revision, we recognize nine Caribbean species out of an estimated 20 *Adiantopsis* species worldwide. In the Caribbean, *Adiantopsis* is a genus primarily of calcareous forests and cliffs. Six of the nine Caribbean *Adiantopsis* species are limited to narrow ecological niches, such as serpentine soils,

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and are endemic to small geographic areas of single islands.

Relative to other cheilanthoid genera, a paucity of information exists about *Adiantopsis*. It is one of many small, overlooked tropical genera that have never been examined using formal taxonomic methods. Holttum (1975: 500) recognized this problem nearly 30 years ago, and called for "New total monographs...to reveal the kinds of groups which can be tackled by the methods of biosystematics." Reasons for studying *Adiantopsis* were simply to describe and enumerate the taxa present, and increase our knowledge of this genus. Such knowledge is a prerequisite for future systematic, molecular, and evolutionary research on *Adiantopsis*. Additionally, taxonomic research on *Adiantopsis* provides data for the eventual reorganization of the polyphyletic *Cheilanthes* Sw. (Gastony, unpublished data) into a natural (i.e., monophyletic) classification scheme, something that is not possible without basic research on *Adiantopsis* and other understudied elements of *Cheilanthes*.

Adiantopsis also possesses a striking range of laminar morphology. The laminae may be palmate (radiate), pedate, or pinnate. This range of variation does not occur in many other fern genera, especially ones as small as *Adiantopsis*. However, without a solid taxonomy of the species, understanding the evolution of this variation is not possible. Thus, another reason for studying *Adiantopsis* was to develop and evaluate hypotheses about the origin of these laminar morphologies.

The results presented in this revision are a component of a complete monograph of *Adiantopsis* that is currently in progress. In this publication, a taxonomic revision of the Caribbean *Adiantopsis* taxa is presented; the Central and South American taxa will be included in a future, more comprehensive monograph. Although this taxonomic treatment deals only with the Caribbean species, the discussion of *Adiantopsis* biology in this revision should apply to the entire genus.

MATERIALS AND METHODS

We examined approximately 500 specimens from the following herbaria for this revision: B, BM, DUKE, F, FI, GH, K, L, MICH, MO, MU, NY, P, UC, and US. In all, 136 characters were scored for each species. For the most part, morphological characters were recorded without disturbing the specimen, and were collected by eye or with a dissecting microscope. An Olympus BH-2 compound light microscope was used to examine microscopic characters. The methodologies for describing characters requiring special preparation are described below.

For length and width measurements, scales of the rhizome, stipe, and rachis were mounted in Hoyer's solution (Anderson, 1954) on a microscope slide. Measurements were made on a compound light microscope. Scales were collected only from specimens with numerous scales, so that specimens would still possess scales for future research.

Guard cell measurements were made with a compound light microscope using prepared laminar tissue. Ultimate divisions were collected from various parts of the frond to avoid any difference in guard cell length attributed to position. The collected laminar tissue was placed into a 30% weight/volume (w/v) NaOH solution for 20 minutes to remove epicuticular wax. To decolorize the tissue, it was taken through an ethanol series of 20%, 50%, 85%, and 100%, and then backward through that series to water. The tissue was kept at each stage of the series for 10 minutes. The decolorized tissue was stained using a modification of Foster's Tannic Acid – Iron Chloride method (Johansen, 1940): decolorized tissue was placed in a 1% w/v aqueous solution of tannic acid for 10 minutes, briefly rinsed in water, and transferred to a 3% w/v aqueous solution of ferric chloride for approximately 30 minutes. The tannic acid and ferric chloride steps were repeated until the cell walls were dark enough to be readily seen. Once the visibility of the cell walls was satisfactory, the tissue was mounted on slides using Hoyer's solution, and guard cell length measurements were made on a compound light microscope.

Sporangia were collected from herbarium specimens using forceps and mounted on a slide with Hoyer's solution. Two measurements were made from collected sporangia: the number of indurated arcus cells, and their height. Data were collected on a compound light microscope.

Spores were collected from herbarium specimens and examined using both Scanning Electron Microscopy (SEM) and light microscopy. Spores for SEM were collected from open sporangia to ensure that the spores were mature and that there were no contaminating spores from other specimens. For counting spore number per sporangium, complete intact sporangia were collected from each specimen. The closed sporangia were collected using fine forceps and transferred to an aluminum SEM stub that was prepared with a double-sided sticky tab and a drop of water. The water allowed the spores to be easily scattered over the surface of the stub and kept the spores on the stub when breaking open intact sporangia. SEM stubs were gold-palladium sputter coated for 90 seconds at 45 milliamps. Spores were examined on a JEOL JSM-T200 SEM at various working distances, voltages, and spot sizes, depending

on the stub. Pictures were taken using an attached Land camera with Polaroid Polapan 55 black and white film. For light microscopy, spores were collected with fine forceps from open sporangia. These spores were mounted on a slide with Hoyer's solution and measured on a compound light microscope.

Data analyses were conducted using SAS (Version 8; SAS, 2000) and OpenOffice.org Calc (Version 1.1; OpenOffice.org, 2003). Guard cell, arcus cell, and spore size data were compared in SAS using one-way ANOVAs with Tukey-Kramer multiple pairwise comparisons ($\alpha = 0.05$) to identify significantly different values. Ranges, means, modes, and standard deviations for all quantitative characters were calculated using OpenOffice.org Calc. Box plots and histograms for select data sets were constructed using OpenOffice.org Calc.

Character terminology in this revision generally follows Lellinger (2002). One deviation is the scoring of planar shapes; these were characterized using the "Symmetric Plane Figures" guide published by the Systematics Association Committee (1962). Additionally, as *Adiantopsis* possesses complex laminar architectures, terms relating to the pinnae and pinnules have been slightly modified from Lellinger (2002). In taxa that are more than bipinnately compound, the term ultimate division, which is not in Lellinger (2002), is used to describe any portion of the lamina that is not further dissected or compound, regardless of its position. Thus, an ultimate division may be a pinna, a pinnule, or a pinnulet, so long as it is not further divided. When using the term ultimate division to describe these various structures, no homology is implied. Thus, pinnae are still the primary division of the lamina, but when pinna morphology is described it applies only to pinnae that are compound themselves (i.e., bipinnate and more compound species). This same logic applies to pinnules. Thus, all final divisions of the lamina are grouped under ultimate division; divisions that are themselves compound are described using standard positional terms (pinna, pinnule, etc.).

ECOLOGY

Adiantopsis species are ecologically variable. Caribbean *Adiantopsis* frequently occur in moist, forested areas, or on moist rock walls, often in gullies or cave entrances. In South America, many species also prefer moist, forested areas, often occurring near streams or on stream banks, although some South American *Adiantopsis*, such as some elements of *A. chlorophylla* (Sw.) T. Moore, do prefer exposed, rocky habitats. An alkaline substrate appears to be a requisite for many *Adiantopsis* taxa. In the

Caribbean, this includes limestone, serpentine, and amphibolite substrates. *Adiantopsis radiata* (L.) Fée may be able to grow in a variety of pH substrates. However, at least one South American species, *A. monticola* (Gardner) T. Moore, prefers acidic substrates. *Adiantopsis* taxa occur from near sea level to as high as 2800 m (Tryon & Stolze, 1989).

MORPHOLOGY

No previous generic-level description of *Adiantopsis* morphology exists. The following description is the first of its sort for the genus. However, it cannot be considered comprehensive as it only represents data and patterns observable from herbarium specimens and excludes possible Old World members.

Adiantopsis is a genus of generally erect, small to large herbaceous ferns. Among the Caribbean species, the plants (as a function of leaf length) range from small (9.5 cm in *A. asplenioides* Maxon) to medium sized (to 74.0 cm in *A. parvisegmenta* M. S. Barker & Hickey); most individuals are around 20–40 cm long. Larger taxa occur in South America, such as *A. chlorophylla* and *A. ×australopedata* Hickey, M. S. Barker & Ponce, that may exceed one and a half meters in length. Most *Adiantopsis* taxa are strict, or stiffly erect. In *A. asplenioides* and *A. paupercula* (Kunze) Fée, the plants are also erect, but the stipes are not as stiff as other taxa. Caribbean *Adiantopsis* taxa are generally smaller than their South American congeners, and less habit variation is observed.

The rhizomes of *Adiantopsis* taxa are all similar. Rhizomes range from erect, to ascending, to decumbent. It is not clear if rhizomes are distinctly subterranean or marginally surficial, but given the amount of soil on most rhizomes they appear to be at least partially hypogeal. In this respect, no difference is observed among taxa. Rhizomes range to 5.9 cm long and 2.3 cm diameter. Persistent, bicolorous scales densely cover the rhizomes (Figure 1A); these may play some role in preventing dessication and/or infection by fungi or bacteria. In all species, a dense tangle of fibrous roots emerges from all sides of the rhizome. Stipes also emerge from all sides of the rhizomes, suggesting a fundamentally radial symmetry (Figure 1A). No positional relationship was observed between the stipes and the roots.

Frond axes in *Adiantopsis* are typically cheilantheid. They are generally persistent and atropurpureous to atrocastaneous, becoming darker at senescence. *Adiantopsis* axes are also carinate adaxially (Figure 1B). These carinae are in the form of paired, golden ridges raised above the surface of the axis (described as "sclerotic ribs" for putative *Adiantopsis* taxa in Ponce & Morbelli, 1989). Tryon

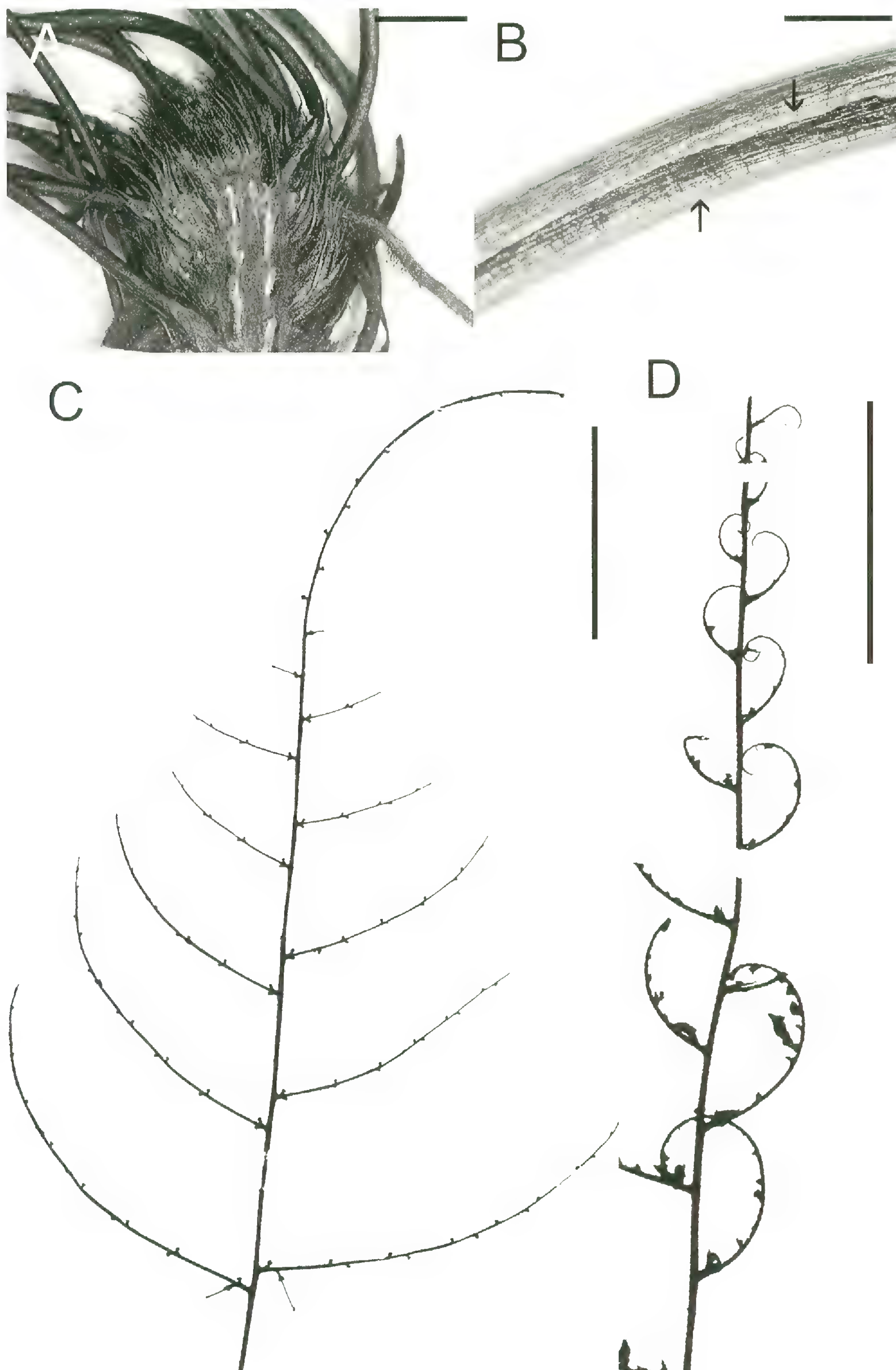


Figure 1. —A. Longitudinal section of *Adiantopsis paupercula* rhizome with bicolorous scales densely covering rhizome surface, and radially attached stipes (C. Wright 961, US). Scale bar = 0.25 cm. —B. Adaxial carinae (indicated by arrows) on *A. reesii* stipe (Ekman 9987, UC). Scale bar = 1.5 mm. —C. Persistent costae of *A. paupercula* (H. A. Hespenheide 1191, US) retaining their original position. —D. Marcescent costae of *A. vincentii* (C. V. Morton 10389, US) curling upon themselves. Scale bars C, D = 2.0 cm.

and Tryon (1982) used the carinae to distinguish *Adiantopsis* from *Cheilanthes*. However, characterization of *Cheilanthes* as lacking carinae is not accurate. Some *Cheilanthes*, such as *C. aemula* Maxon, *C. microphylla* (Sw.) Sw., and *C. wrightii* Hook. are adaxially bicarinate (Barker, pers. observ.). In the bicarinate *Cheilanthes*, the carinae are usually green or pale green, approaching the color of the laminar tissue, whereas *Adiantopsis* carinae are distinctly golden, independent of laminar color. Furthermore, carinae in *Cheilanthes* are typically restricted to the costae and costules, whereas in *Adiantopsis* they generally occur on all axes. Additionally, *Cheilanthes* carinae are contiguous with the laminar tissue. In *Adiantopsis*, with the exception of lamina and pinnae apices, carinae remain distinct from the laminar tissue. However, this may be more an architectural phenomenon than a reflection of the absence of homology. Thus, carinae distinguish *Adiantopsis* from *Cheilanthes* by their form, not their presence.

Of all axis characters, those associated with the stipes are the most taxonomically informative. In *Adiantopsis*, the stipes may grow to 47.0 cm long and 2.6 mm in diameter. Pneumatophores were observed on stipes of all species. Taxonomic differences emerge when comparing the ratio of stipe length to overall frond length. In the pinnate Caribbean taxa, stipes are one third the overall frond length, whereas they are equal to or longer than the lamina in the pedate taxa. Stipes of *A. radiata* are consistently longer than the lamina, and in *A. paupercula* they approach equity with laminar length, being variously shorter or longer than the lamina. There are also taxonomic differences in the extent of carinae development. In *A. paupercula*, the carinae begin in the upper half of the stipe, frequently starting at the stipe mid-point. Carinae begin in the upper third and quarter of stipes in *A. pentagona* M. S. Barker & Hickey and *A. rupicola* Maxon. In *A. parvisegmenta*, *A. pedata* (Hook.) T. Moore, *A. reesii* (Jenm.) C. Chr., and *A. vincentii* M. S. Barker & Hickey, carinae begin at the stipe bases or in the basal half of stipes. *Adiantopsis radiata* frequently lacks carinae on the stipes, but when present, they begin at the base of the stipe. Carinae are always absent on the stipes of *A. asplenoides*.

Laminar axes in *Adiantopsis* are generally persistent. In most taxa, the original laminar axis position and form are retained even after the loss of ultimate divisions (Figure 1C). However, in senescent fronds of *A. rupicola* and *A. vincentii* the costae are marcescent and curl upon themselves becoming almost circinate in appearance (Figure 1D).

In his revision of *Lindsaea* Dryand. ex Sm., Kramer (1957: 123) noted that "In few fern genera such a great diversity of leaf-pattern is found as in *Lindsaea*." If

the above statement is true for *Lindsaea*, then *Adiantopsis* may have the largest diversity of laminar variation seen in any fern genus, and it is certainly the most diverse among the cheilanthoid genera. Three basic laminar architectures occur in *Adiantopsis*; palmate, pinnate, and pedate (Figure 2). The palmate architecture is observed only in *A. radiata* (Figure 2A). In this species, the pinnae are born from a single point at the stipe apex, and no noticeable rachis is present. A pinnate laminar architecture occurs in *A. asplenoides*, *A. parvisegmenta*, *A. paupercula*, *A. reesii*, *A. rupicola*, and *A. vincentii* (Figure 2B). *Adiantopsis pedata*, *A. pentagona*, and *A. australopedata* are pedate (Figure 2C). As in pinnate species, the pinnae of pedate laminae are disposed along a central rachis. However, in the pedate taxa, the basal basiscopic pinnules of the first pinnae pair are considerably longer than the other pinnules. In the pinnate and pedate taxa, the lamina lies in the same plane as the stipe and rachis. However, in palmate *A. radiata*, the lamina is geniculate to the stipe.

The overall shape of *Adiantopsis* laminae is a reflection of architecture. Palmate *Adiantopsis radiata* has an orbiculate lamina. Pinnate taxa are variously triangular to lanceolate, or linear in *A. asplenoides*. Both pedate taxa are pentagonal, as reflected in the name of *A. pentagona*. Laminar apices in the pinnate and pedate taxa are difform, with the exception of *A. paupercula*, which is conform.

The laminae in *Adiantopsis* range from small and simple to large and complex. *Adiantopsis asplenoides* has the smallest laminae, with a maximum length of 14.5 cm and a width of 1.1 cm. It is also the simplest, with pinnate-pinnatifid to bipinnate laminae. Of the Caribbean taxa, *A. reesii* has the longest laminae at 60.0 cm, whereas the widest laminae are in *A. pentagona* at 48.2 cm wide. *Adiantopsis parvisegmenta* and *A. paupercula* may have quadripinnate laminae and are the most compound among Caribbean *Adiantopsis* taxa. However, in South America, laminae may be pentapinnate as in *A. chlorophylla*. With the exception of *A. asplenoides*, most Caribbean *Adiantopsis* laminae are 20–40 cm long and 10–20 cm wide.

Adiantopsis laminar tissues vary from papyraceous to spongiouse. Papyraceous laminar tissues are found in *A. reesii* and *A. vincentii*. *Adiantopsis asplenoides* and *A. pedata* are chartaceous. *Adiantopsis rupicola* may have chartaceous to thin-spongiouse tissue, whereas *A. radiata* and *A. pentagona* have thin-spongiouse tissue. Finally, spongiouse laminar tissue is found in *A. parvisegmenta* and *A. paupercula*.

Randomly dispersed on the adaxial laminar surface are white epidermal cells. These cells are hard, and probably calcified. Hydathodes are also located on the

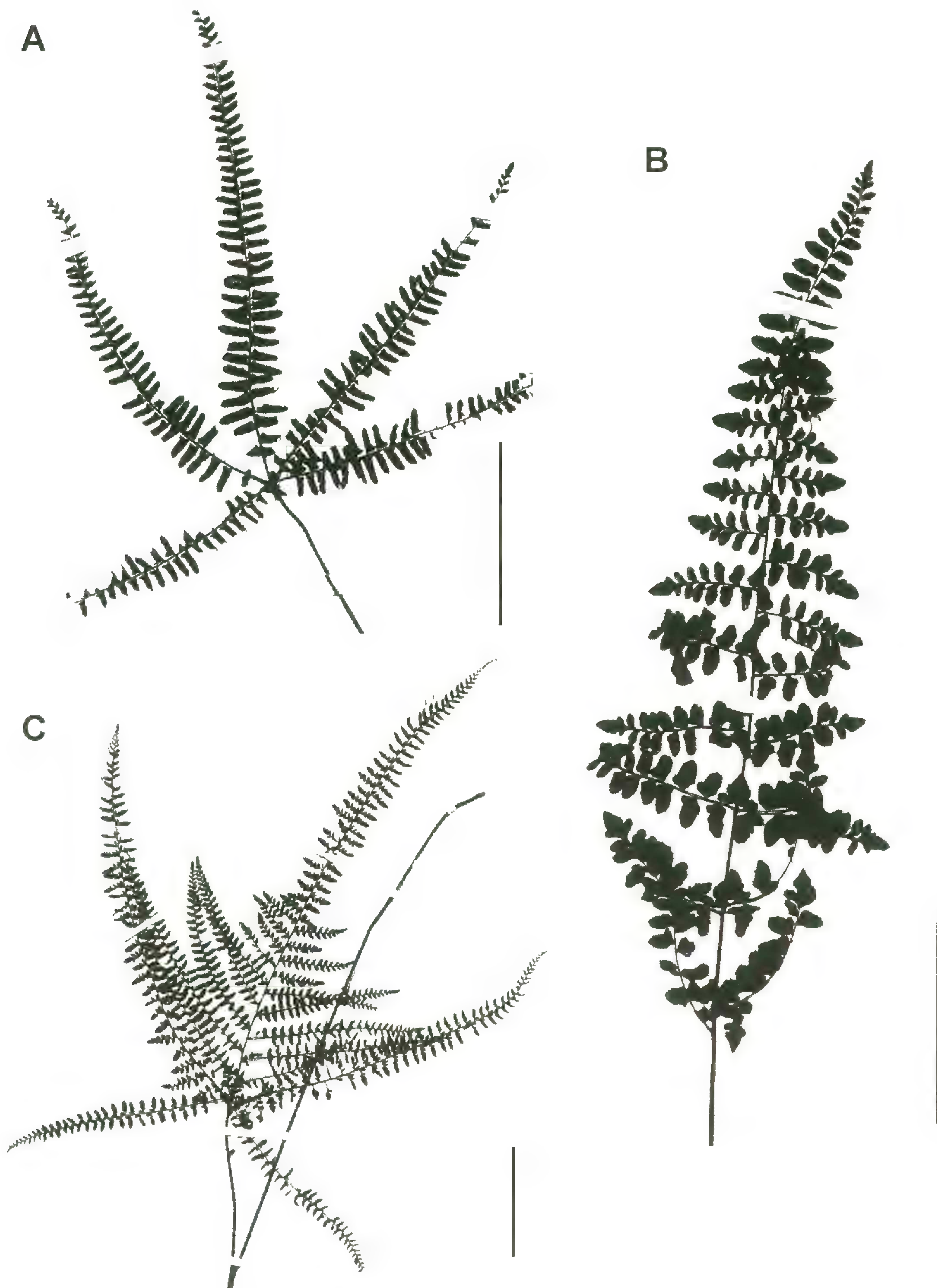


Figure 2. —A. Radiate lamina morphology of *Adiantopsis radiata* (J. L. Main s.n., MU). —B. Pinnate lamina morphology of *A. rupicola* (W. Palmer 242 & J. H. Riley, US). —C. Pedate lamina morphology of *A. pentagona* (C. Wright 3949, MO). Scale bars = 5 cm.

Table 1. Sample sizes, means, standard deviations, and ranges (min, max) for Caribbean *Adiantopsis* guard cell lengths. Taxa that do not share letters are significantly different from each other ($P < 0.0001$).

Taxon	Sample size	Mean (μm)	Standard deviation (μm)	Min (μm)	Max (μm)
<i>A. asplenoides</i> ^a	50	52.42	3.78	45.64	57.05
<i>A. parvisegmenta</i> ^a	125	45.5	4.44	32.6	58.68
<i>A. paupercula</i> ^b	125	61.22	5.59	48.9	68.46
<i>A. pedata</i> ^c	125	65.86	5.88	53.79	78.24
<i>A. pentagona</i> ^c	125	67.04	8.85	32.6	83.13
<i>A. radiata</i> ^a	125	49.77	1.95	35.86	63.57
<i>A. reesii</i> ^a	125	44.34	4.49	32.6	53.79
<i>A. rupicola</i> ^a	125	49.75	1.32	42.38	57.05
<i>A. vincentii</i> ^a	50	45.84	3.53	40.75	53.79

adaxial surface of the laminar tissue. In *Adiantopsis*, these hydathodes are sub-marginal on single vein tips, and are generally covered with a hard, amorphous, white mass. As *Adiantopsis* prefers calcareous substrates, this material appears to be a guttation by-product. This material, and the wall constituents of the white epidermal cells, is most likely calcium or some other mineral collected from the substrate.

Guard cells are located only on the abaxial side of the laminar tissue and are anomocytic. They may be surrounded by two, three, four, or as many as five subsidiary cells, even on the same ultimate division. Length differences do exist among the guard cells of different taxa (Table 1). The guard cells of *A. asplenoides*, *A. parvisegmenta*, *A. radiata*, *A. reesii*, *A. rupicola*, and *A. vincentii* form a group of taxa with guard cell length means centering around 45 μm. *Adiantopsis paupercula* has a mean guard cell length of 61.22 μm, whereas *A. pedata* and *A. pentagona* form a group of taxa with a combined mean guard cell length of 66.45 μm. The guard cell lengths of all three groups are significantly different from each other ($P < 0.0001$) in Tukey-Kramer pairwise comparisons.

Pinnæ in *Adiantopsis* are generally triangular to fusiform. The triangular basal pinnæ of the pedate taxa are strongly inequilateral, a function of the much extended basal basiscopic pinnules. All other pinnæ of the pedate taxa are more or less equilateral. In *A. parvisegmenta* and *A. paupercula*, pinnæ are also somewhat inequilateral with basiscopic pinnules slightly longer than the acroscopic pinnules (Figure 1C). Pinnæ of *A. asplenoides* reach 6.1 mm long and 6.0 mm wide. Those of other species range to 24.1 cm long and to 19.9 cm wide. Pinnæ are alternate, with the exception of the subopposite basal pinnæ of the pedate taxa. In *A. radiata*, the pinnæ radiate from the stipe apex. Pinnæ in *Adiantopsis* are generally ascending, but a number of taxa also have patent pinnæ. In *A. parvisegmenta*, *A. paupercula*, *A. reesii*, *A. rupicola*, and *A. vincentii* the proximal pinnæ are frequently or occasionally arcuate, with only the

distal pinnæ straight. This is quite different from the curling observed in senescent fronds of *A. rupicola* and *A. vincentii* (Figure 1D). In these taxa, the incurved pinnæ increase their curvature dramatically becoming circinate in appearance. In all other taxa, the senescent pinna axes retain their shape, whether straight or somewhat incurved.

Adiantopsis venation and architecture is anadromous. Pinnules are typically narrowly triangular to linear, and occasionally lanceolate. In the pinnate taxa, the basiscopic pinnules are slightly longer than the acroscopic pinnules and may be up to 7.5 cm long and 2.5 cm wide. The basal basiscopic pinnules of the pedate taxa are much longer and reach 15.3 cm in length. Pinnules may be patent to ascending.

Adiantopsis ultimate divisions are an important source of taxonomic information. For example, the ultimate divisions of *A. paupercula* are strongly articulate, with a clear enlargement and differentiation of the axis at its juncture with the laminar tissue (Figure 3A). The ultimate divisions of other *Adiantopsis* taxa, while articulate with age, lack the swollen and distinct articulation point of *A. paupercula* (Figure 3B). The ultimate divisions of *A. parvisegmenta* are by far the smallest of the Caribbean taxa, reaching a maximum size of 3.5 mm long by 2.5 mm wide. The ultimate divisions of other *Adiantopsis* taxa generally overlap in size, with a maximum length of 13.5 mm in *A. radiata* and maximum width of 4.5 mm in *A. paupercula*. There is considerable overlap in ultimate division shapes among Caribbean *Adiantopsis*, with shapes ranging from oblong, to oblanceolate, lanceolate, elliptic, trullate, and rhombic. Ultimate division bases are generally cuneate and are often uniauriculate on the acroscopic side. The apices of *A. reesii* and *A. pedata* ultimate divisions are acute and distinctly toothed, whereas in other taxa they are generally acute to round and entire. *Adiantopsis asplenoides* ultimate divisions are distinctly lobed, whereas the margins of other taxa are entire to crenulate (Figure 3C, D, E). All ultimate divisions are

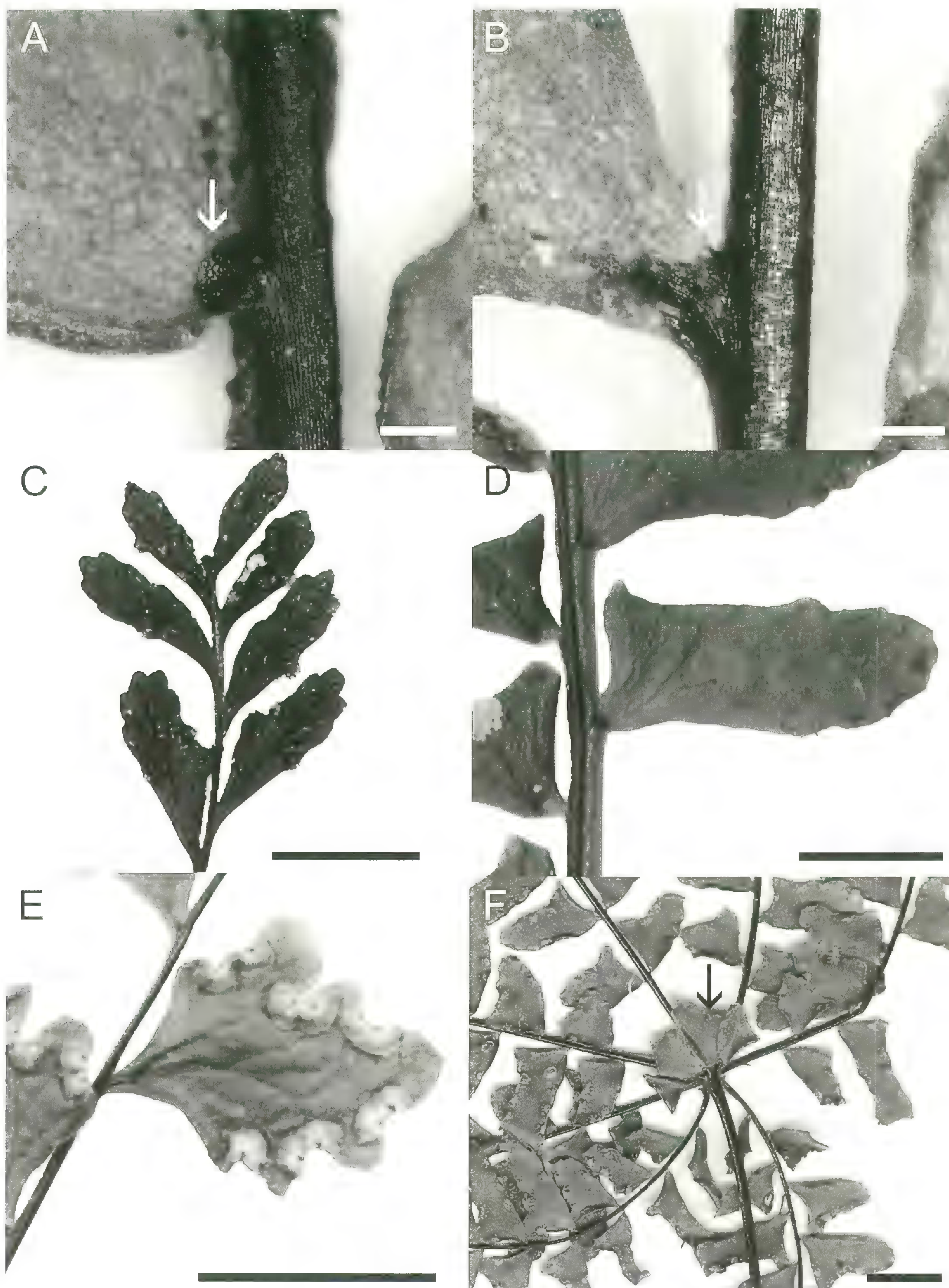


Figure 3. —A. Swollen stalk apex at junction with lamina tissue (arrow) of *Adiantopsis pauperula* (C. Wright 962, UC). Ultimate divisions are articulate and break cleanly at this swollen point. Scale bar = 1 mm. —B. Non-swollen stalk apex at junction with lamina tissue (arrow) of *A. pentagona* (J. G. Jack 7903, US). Ultimate divisions are articulate, but do not break cleanly from the stalk. Scale bar = 0.3 mm. —C. Toothed ultimate division apices of *A. reesii* (E. L. Ekman 10603, US). —D. Round, entire ultimate division apices of *A. radiata* (J. A. Shafer 3777, F). —E. Lobed ultimate divisions of *A. asplenioides* (Bro. Alain 1226 & Acuna, US). —F. Abaxial view of basal flabellate divisions of *A. radiata* (G. L. Webster 13425, MICH), indicated by arrow. The divisions are attached to the stipe apex between pinna pairs. Note similarity of shape between basal ultimate and flabellate divisions. Sori are visible on these basal flabellate divisions, which suggests they are homologous to ultimate divisions of the pinnae. Scale bars C-F = 0.5 cm.

deciduous with persistent stalks ranging from 0.1–6.3 mm in length.

Adiantopsis radiata possesses basal flabellate divisions, an autapomorphy for this taxon. As their name implies, these divisions are generally flabellate and occur on the stipe apex between pinnae (Figure 3F). These basal flabellate divisions appear to be homologous to ultimate divisions. The overall shape of basal pinnules and these flabellate divisions is similar (Figure 3F). Additionally, the basal flabellate divisions become fertile with the other ultimate divisions. They are likely a by-product of axial compression in *A. radiata*, as they appear to be ultimate divisions developed within the stipe crown at a point below the stipe surface. These basal flabellate divisions are usually restricted to mature *A. radiata* plants with larger than average fronds and more than five pinnae.

Adiantopsis indument consists of hairs and scales. The hairs are septate-capitate, with well defined septa and bulbous apical cells. On the axes, they are concentrated at axis junctions and distributed diffusely across the abaxial surface. They are generally appressed and may be up to ten cells long, although most are much shorter. Septate-capitate hairs are also found on the abaxial laminar tissue. Typically, the laminar hairs are three celled, although rarely may they be two or four celled. These septate-capitate hairs are clavate, with an elongate basal cell, a relatively short middle cell, and a bulbous apical cell. In some taxa, such as *A. parvisegmenta*, the apical cell is very bulbous and overarches the middle cell. In *A. pentagona* and others, the apical cell, while still bulbous, is generally elongate and does not overlap the middle cell. The basal cells are usually clear, but the middle and apical cells are variable, being red, gold, white, or clear, but usually the two are not the same color. While some taxonomic trends in color have been observed, they are too variable to reliably differentiate taxa. These septate-capitate hairs are present in some putative South American *Adiantopsis* taxa as well and apparently demonstrate some taxonomic utility (Ponce & Morbelli, 1989). Their ultimate taxonomic use within the genus can be re-evaluated once all *Adiantopsis* taxa have been fully examined.

The type of hairs observed in *Adiantopsis* appears to be a synapomorphy for the genus. Tryon and Tryon (1982) stated that *Adiantopsis* is closely related to the *Cheilanthes microphylla* group of *Cheilanthes*. However, a number of differences between the hairs of the two groups are observed. Hairs of the *C. microphylla* group are much longer, more filamentous, and with indistinct or oblique cross walls, characteristics not associated with *Adiantopsis*. In the *C. microphylla*

group, both adaxial and abaxial surfaces of the lamina and axes are covered with hairs, whereas in *Adiantopsis* the hairs are restricted to abaxial surfaces. Additionally, hairs in the *Cheilanthes* taxa are much denser than *Adiantopsis* hairs. The septate-capitate hairs of *Adiantopsis* have not yet been observed in *Cheilanthes*.

Adiantopsis scales are found on the rhizome, stipe, and laminar axes. Rhizome scales are bicolorous (Figure 1A), with persistent, black to dark brown centers and deciduous, golden or, in *A. asplenioides*, white, translucent margins. Scales densely cover the rhizome surface. These scales are generally lanceate to acicular, with truncate bases, entire to slightly repand margins, and acute, gland tipped apices. The rhizome scales of all species are similar and generally lack taxonomic value.

Stipe scales are uniformly concolorous and tan. Overall, the scales range from lanceolate to acicular, or occasionally subulate. *Adiantopsis* stipe scales are frequently biauriculate and appear pseudopeltate, but some scale bases are not auriculate and are truncate. Scale margins range from entire to slightly repand. Apices are acute to attenuate and gland tipped. In all taxa, stipe scales are deciduous, as the remnants of scale bases are often observed and the number of scales varies considerably. These scale characters possess relatively little taxonomic value. However, the stipe scales of *A. parvisegmenta*, *A. paupercula*, *A. reesii*, *A. rupicola*, and *A. vincentii* are divergent from the stipe surface, whereas *A. pedata*, *A. pentagona*, and *A. radiata* stipe scales are appressed to the stipe surface, only occasionally divergent. Stipe scales are distributed at the base of stipes, typically to a maximum of 7.1 cm above the rhizome. However, stipe scales on some *A. reesii* specimens are distributed along the entire length of the stipe to the rachis. It is possible that stipe scales are distributed higher on the stipes of other taxa and are simply not observed because of their deciduous nature. Stipe scales are conspicuously absent in *A. asplenioides*.

Distal to the stipe, scales are rarer, more easily overlooked, and are usually no more than five cells wide and eight cells long. They are concentrated at laminar axis junctions and are diffusely scattered on abaxial axis surfaces. Scales are typically lanceate in overall shape and are gland tipped. Some scales are biseriate and closely resemble axis hairs, suggesting that hairs and scales in *Adiantopsis* form a developmental and evolutionary continuum. Laminar scales are not taxonomically informative.

Venation in *Adiantopsis* is free. In most species, veins are pseudodichotomous and anadromous, although in *A. paupercula* veins are flabellate. Veins are typically obscure to occult and are generally im-

mersed in the laminae. Veins always terminate marginally or sub-marginally in adaxial hydathodes.

Adiantopsis sori are marginal and consistently uninerved. Sori occur on both acroscopic and basiscopic division margins; in *A. asplenoides* they frequently occur on the interior sides of lobes. For the most part, a single, distinct pseudindusium covers each sorus, although in *A. asplenoides*, pseudindusia may be partially confluent across sinus bases. The generally distinct pseudindusia distinguish *Adiantopsis* from *Cheilanthes*, in which a series of confluent pseudindusia comprise the entire margin of an ultimate division (Tryon & Tryon, 1982). *Adiantopsis* pseudindusia are typically lunate to quadrangular, with entire to erose margins.

Sporangia in *Adiantopsis* show a mixed development and are generally subglobose and long stalked. The stalks are typically three cells long. However, in *A. asplenoides*, and an undescribed Bolivian and Paraguayan taxon, the sporangia are globose and essentially sessile, with apparently only a single cell layer between the sporangium and receptacle. The number of indurated arcus cells shows taxonomically informative trends in *Adiantopsis*. Indurated arcus cell numbers show narrow ranges of variation, with modes that are useful for discriminating among taxa (Figure 4). For example, *A. pedata*, *A. reesii*, and *A. vincentii* have a mode of 14, *A. parvisegmenta*, *A. paupercula*, *A. pentagona*, and *A. rupicola* have a mode of 16, *A. asplenoides* has a mode of 11, and *A. radiata* has a mode of 20. *Adiantopsis* sporangia generally contain 64 spores; however *A. asplenoides* has 32 spores per sporangium.

Indurated arcus cell sizes also differentiate taxa into two groups (Table 2). One group consists of the pedate taxa, with a mean indurated arcus cell height of approximately 48 μm . All other taxa are included in the second group, with a mean indurated arcus cell height of approximately 38 μm . These two groups were significantly different from each other in Tukey-Kramer pairwise comparisons.

Adiantopsis spores are tetrahedral-globose and generally echinate (Figure 5). The only species to deviate from this is *A. asplenoides*, which has cristate spores with anastomosing strands below the muri (Figure 5B). Among the echinate spored species, some notable differences are observed. The echinae bases of *A. pedata*, *A. pentagona*, and *A. radiata* are all dissected, whereas the echinae bases in other taxa are complete. Also, the echinae of *A. paupercula* spores are more compact relative to the echinae of other species' spores. The laesurae are obscured by the ornamentation in all spores except *A. asplenoides*; its laesurae are easily observed with a dissecting microscope. Spore sizes in *Adiantopsis* are divided

into three distinct groups all statistically different from each other, as determined by Tukey-Kramer pairwise comparisons (Table 3). The first group, with spore lengths averaging around 37 μm , includes *A. parvisegmenta*, *A. paupercula*, *A. radiata*, *A. reesii*, *A. rupicola*, and *A. vincentii*; *Adiantopsis pedata* and *A. pentagona* compose the second group with average spore lengths of approximately 46 μm . Finally, *A. asplenoides* forms a third group, with a mean spore length of 75.83 μm .

The echinate spores of *Adiantopsis* help distinguish it from *Cheilanthes*. The spore ornamentation of *Cheilanthes* is variable, with only a few Australian species possessing echinate spores (Tryon & Tryon, 1982). Even in light of these echinate Australian *Cheilanthes*, Tryon and Tryon (1982) recognized *Adiantopsis* based primarily on the echinate spore ornamentation, as the echinate Australian *Cheilanthes* are easily distinguished from *Adiantopsis* by vegetative characters. The only exception to echinate spores in Caribbean *Adiantopsis* is *A. asplenoides*. Given its other unique characters, *A. asplenoides* may belong in another, perhaps new, genus, although some putative South American *Adiantopsis* taxa that are currently placed in *Cheilanthes* also have cristate spores (Ponce & Morbelli, 1989). *Adiantopsis asplenoides* is retained here only until a full analysis of South American *Adiantopsis* is completed. If *A. asplenoides* is segregated from *Adiantopsis*, echinate spores would characterize the genus.

TAXONOMIC HISTORY

In 1852, Fée erected the genus *Adiantopsis* for various species in *Adiantum* L., *Cheilanthes*, and *Hypolepis* Bernh. with distinct pseudindusia for each sorus. Originally, Fée included four species in *Adiantopsis*: *A. capensis* (Sw.) Fée, *A. chlorophylla*, *A. paupercula*, and *A. radiata*. He designated *A. paupercula* as the type species for the genus. Christensen (1906) later lectotypified the genus with *A. radiata*; this was unnecessary because Fée (1852: 145) clearly designated (with the term *Diagnosis*) *A. paupercula* by referencing Kunze's (1850) publication of the species. As a result, some authors (e.g., Mickel & Smith, 2004) recognize *A. radiata* as the type, whereas others (e.g., Tryon & Tryon, 1982; Proctor, 1985) recognize *A. paupercula*. It seems clear to us that *A. paupercula* should be recognized as the type species for the genus, as Fée unambiguously designated it as such.

Fée (1857) also published two subgenera within *Adiantopsis*: *Euadiantopsis* Fée (= *Adiantopsis*) and *Cheilanthesastrum* Fée. Although he did not provide characters for the subgenera, an evaluation of the list

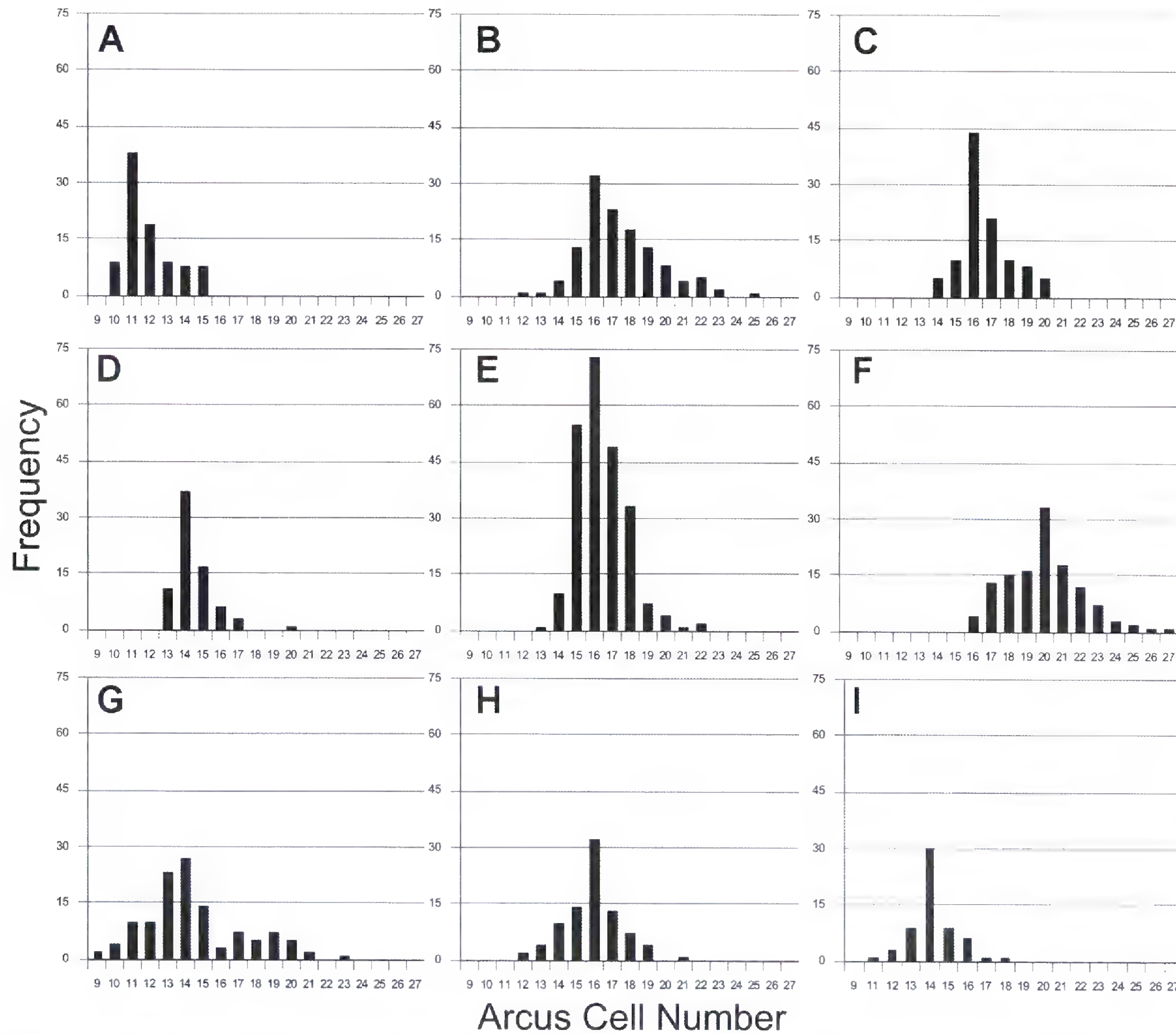


Figure 4. Frequency histograms of *Adiantopsis* arcus cell number. X-axis is arcus cell number, Y-axis is frequency (absolute value). —A. *A. asplenoides*. —B. *A. parvisegmenta*. —C. *A. paupercula*. —D. *A. pedata*. —E. *A. pentagona*. —F. *A. radiata*. —G. *A. reesii*. —H. *A. rupicola*. —I. *A. vincentii*.

Table 2. Sample sizes, means, standard deviations, and ranges (min, max) for Caribbean *Adiantopsis* arcus cell height. Taxa that do not share letters are significantly different from each other ($P < 0.0001$).

Taxon	Sample size	Mean (μm)	Standard deviation (μm)	Min (μm)	Max (μm)
<i>A. asplenioides</i> ^a	50	34.38	2.47	30.97	39.12
<i>A. parvisegmenta</i> ^a	125	40.78	3.19	32.6	48.9
<i>A. paupercula</i> ^a	125	40.59	3.3	35.86	47.27
<i>A. pedata</i> ^b	125	48.8	3.55	40.75	55.42
<i>A. pentagona</i> ^b	125	48.66	4.46	40.75	58.68
<i>A. radiata</i> ^a	125	39.04	2.76	30.97	46.46
<i>A. reesii</i> ^a	125	36.34	6.47	21.19	48.9
<i>A. rupicola</i> ^a	125	37.16	3.33	32.6	42.38
<i>A. vincentii</i> ^a	50	38.01	4.31	32.6	52.16

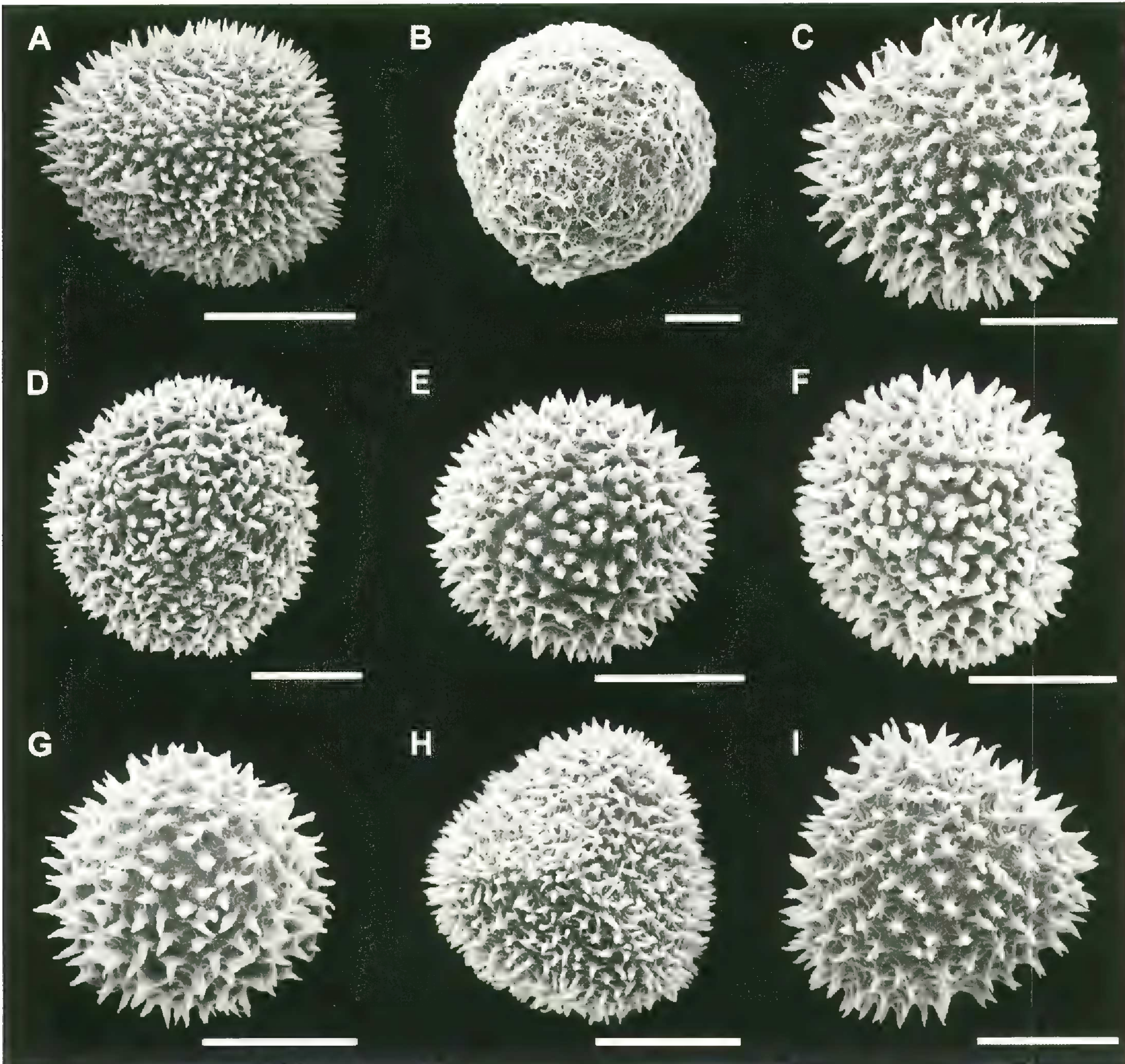


Figure 5. Electron micrographs of Caribbean *Adiantopsis* spores. —A. Echinate *A. radiata* spore with dissected echinae bases (J. A. Shafer 3777, F). —B. Cristate *A. asplenioides* spore with anastomosing strands beneath the muri (Br. Alain 41226, US). —C. Echinate *A. parvisegmenta* spore with complete echinae bases (J. G. Jack 6877, US). —D. Echinate *A. paupercula* spore with compact echinae (Maxon 4239, US). —E. Echinate *A. reesii* spore with complete echinae bases (E. L. Ekman 9987, F). —F. Echinate *A. rupicola* spore with complete echinae bases (Britton et al. 3497, US). —G. Echinate *A. vincentii* spore with complete echinae bases (Egger 5399, F). —H. Echinate *A. pedata* spore with dissected echinae bases (Harris 10878, US). —I. Echinate *A. pentagona* spore with dissected echinae bases (C. Wright 3949, US). Scale bars = 20 μm.

Table 3. Sample sizes, means, standard deviations, and ranges (min, max) of Caribbean *Adiantopsis* spore lengths. Taxa that do not share letters are significantly different from each other ($P < 0.0001$).

Taxon	Sample size	Mean (μm)	Standard deviation (μm)	Min (μm)	Max (μm)
<i>A. asplenoides</i> ^a	50	75.83	6.74	58.68	88.02
<i>A. parvisegmenta</i> ^a	125	40.59	2.41	34.23	47.27
<i>A. paupercula</i> ^b	125	41.4	2.96	35.86	45.64
<i>A. pedata</i> ^c	125	45.5	3.85	38.31	54.61
<i>A. pentagona</i> ^c	125	45.77	3.4	40.75	58.9
<i>A. radiata</i> ^b	125	39.94	2.35	34.23	47.27
<i>A. reesii</i> ^b	125	36.34	2.44	30.97	44.83
<i>A. rupicola</i> ^b	125	37.75	1.68	34.23	40.75
<i>A. vincentii</i> ^b	50	38.16	3.67	32.6	44.01

of species he included in each subgenus identified possible distinguishing characters. Subgenus *Euadiantopsis* (*Adiantopsis radiata*, *A. paupercula*, and *A. pteridoides* Moore [= *Cheilanthes pteridoides* Sw.]) is apparently characterized by more oblong ultimate divisions, whereas those of subgenus *Cheilanthastrum* (*Adiantopsis chlorophylla*, *A. spectabilis* [= *A. chlorophylla*], and *A. capensis* [= *Cheilanthes capensis*]) are more elliptic to oblanceolate. Additionally, two of the taxa in subgenus *Euadiantopsis*, *A. paupercula* and *A. radiata*, have ultimate division shapes that are more like those found in *Adiantum* than in *Cheilanthes*, whereas the species placed in subgenus *Cheilanthastrum* have ultimate division shapes more similar to *Cheilanthes*. Although these subgenera are not recognized here, they do reflect morphological trends that have caused taxonomic confusion in the past.

Past authors have not always recognized *Adiantopsis*. For example, Hooker and Baker (1883) placed *Adiantopsis* as a subgenus within *Cheilanthes* in their *Synopsis Filicum*. However, they did use Fée’s (1852) characters to recognize subgenus *Adiantopsis*. The placement of *Adiantopsis* within *Cheilanthes* is in line with their overall generic concept, which recognized a small number of large fern genera with a substantial number of subgenera. Copeland (1947) also did not recognize *Adiantopsis*, suggesting that it was insufficiently distinct to warrant generic status; he placed it in synonymy under *Cheilanthes*.

Other authors have recognized *Adiantopsis*, but with qualification. For example, Smith (1981) suggested that if species such as *A. chlorophylla* and *A. seemannii* (Hook.) Maxon are included in *Adiantopsis*, the distinction between it and *Cheilanthes* disappears. Specifically, he cited the morphological similarities of these species to *C. aemula* and *C. microphylla*.

Many other researchers have recognized *Adiantopsis* as construed by Fée. Christensen (1906) recognized it in his *Index Filicum*. Maxon (1908) also recognized *Adiantopsis* and published a useful synop-

sis of the Cuban taxa. Most modern tropical fern floras recognize *Adiantopsis* as distinct from *Cheilanthes* (Sehnem, 1959, 1961, 1972; Tryon & Tryon, 1982; Proctor, 1985; Lellinger, 1989; Proctor, 1989; Tryon et al., 1990; Pacheco, 1995; Mickel & Smith, 2004). In general, these researchers, and Fée, utilized a more narrowly defined generic concept than either Hooker and Baker (1883) or Copeland (1947). Only Copeland (1947) articulated problems with the recognition of *Adiantopsis*, although he did not refer to a number of distinctive characters, such as spore ornamentation, adaxial carinae, and hair morphology.

Although *Adiantopsis* has been included in many fern floras and indices, little comprehensive research has been done at the species level. One of the most significant contributors to species level taxonomy in *Adiantopsis* was Sehnem. He published a series (1959, 1961, 1972) of keys and species descriptions for various floras in southeastern Brazil and the tri-border region of Argentina, Brazil, and Paraguay. In these treatments, he provided excellent keys to the species of the region using characters that were overlooked by other pteridologists. Further, he provided some clarification to the *A. chlorophylla* species complex by recognizing two new species, *A. perfasciculata* and *A. occulta*. Unfortunately, most pteridologists, including Tryon and Tryon (1982), were unaware of Sehnem’s *Adiantopsis* research.

Tryon and Tryon (1982) were the most recent taxonomists to review *Adiantopsis*. They regarded the genus as closely related to their *Cheilanthes microphylla* group (their *Cheilanthes* group 1). That group and *Adiantopsis* share dark axes and less hair than other cheilanthoid groups. The main character used by Tryon and Tryon (1982) to distinguish *Adiantopsis* from *Cheilanthes* was the echinate spores in *Adiantopsis*. Additionally, they noted adaxially bicarinate laminar axes, asymmetrical and articulate ultimate divisions, and distinct indusia covering single sori as distinguishing features of *Adiantopsis* (Tryon & Tryon, 1982).

Tryon and Tryon (1982) recognized seven *Adiantopsis* species in total, including *Adiantopsis paupercula*, *A. pedata*, *A. radiata*, and *A. reesii* from the Caribbean. In their treatment, they sank *A. rupicola* into *A. reesii*, stating that it does not appear to be distinct, and considered *A. asplenioides* to be a juvenile form of *A. paupercula*. With regard to South American taxa, Tryon and Tryon (1982) did recognize one of Sehnem's species, *A. minutula*, but did not acknowledge his *A. perfasciculata* and *A. occulta*. It is not clear why they did not recognize these two distinctive species. Although Tryon and Tryon's (1982) treatment of *Adiantopsis* failed to mention some key species, they provided the most comprehensive overview of the genus ever published.

Recent molecular work by Gastony (unpublished data) supports the generic status of *Adiantopsis*. A molecular analysis with *rbcL* DNA sequences supports a sister relationship between *A. radiata* and the South American *A. chlorophylla* with 23 synapomorphies and 100% bootstrap support (Gastony, unpublished data). The analysis included representatives of cheilanthoid genera from all geographic regions and provides support that *Adiantopsis* is a distinct genus. Further, it refutes Smith's (1981) contention that including *A. chlorophylla* in *Adiantopsis* makes the genus indistinguishable from *Cheilanthes* because of morphological similarity to *C. aemula*. *Cheilanthes aemula* was included in Gastony's (unpublished data) analysis and was distantly related to the *Adiantopsis* group. Thus, it appears that any morphological similarity observed by Smith (1981) between the two taxa is likely convergent. Additional molecular research with a broader sampling of *Adiantopsis* is needed to evaluate the boundaries of the genus, but it does appear to be phylogenetically distinct from other *Cheilanthes*.

SPECIES CONCEPT

In this revision of *Adiantopsis*, a morphological species concept was employed to discriminate species. Essentially, if groups of collections were morphologically distinct they were recognized as distinct taxa; if not, they were maintained as a single species. Implicit in this usage of the morphological species concept is the assumption that morphological distinctness reflects underlying genetic distinctness produced as a result of unique evolutionary histories for each species. If future research using molecular data, such as population genetic markers that sample multiple loci across the genome, does not identify partitioned genetic variation, then species boundaries should be re-evaluated.

EVOLUTIONARY RELATIONSHIPS

Based on a comparison of morphological data obtained from Caribbean collections, a total of nine morphological species are recognized for this region. Of these nine species, seven are putative diploids and two are putative polyploids. In *Adiantopsis*, chromosome counts are known only from *A. radiata*. The counts of $n = 30$ (Walker, 1973; Smith & Foster, 1984) represent the base number for the cheilanthoid genera, and thus it is assumed that *A. radiata* is a diploid species. As material was not available to count the chromosomes of other *Adiantopsis* taxa, indirect estimates of ploidy level were used. Barrington et al. (1986) demonstrated that guard cell and spore lengths in leptosporangiate ferns frequently correspond to ploidy level. Indurated arcus cell size has also been correlated with ploidy level by Butters and Tryon (1948). Using these cell sizes and spore length (Tables 1, 2, 3), the ploidy levels of *Adiantopsis* taxa were estimated, with *A. radiata* serving as a reference for the diploid ploidy level. These data partition the nine species into two statistically significant groups. All pinnate taxa and *A. radiata* form a group of putative diploid species, whereas the two pedate taxa appear to be polyploid species, most likely tetraploids. The pedate taxa consistently possess larger cell sizes. The cell length differences between putative diploid and tetraploid *Adiantopsis* taxa are comparable to differences observed between diploid and tetraploid leptosporangiate ferns by Barrington et al. (1986) and Butters and Tryon (1948). Based on these data, *A. pedata* and *A. pentagona* are supported as tetraploid species, whereas all other Caribbean taxa appear to be diploid.

Two exceptions to this pattern in cell size exist. Guard cells of *Adiantopsis paupercula* are somewhat larger than all other putative diploid taxa, but not quite as large as those of the putative tetraploid taxa (Table 1). Spore and indurated arcus cell size place this species with the putative diploid taxa (Tables 2, 3). It is not clear why its guard cells show this intermediacy. Given that its spore and indurated arcus cell sizes are within the putative diploid range, it seems probable that this is a diploid taxon and that its guard cell lengths are influenced by other, unknown factors.

The other exception is *Adiantopsis asplenioides*, a species with a number of unique characteristics among Caribbean *Adiantopsis*. Guard cell and indurated arcus cell sizes group this taxon with other putative diploids (Tables 1, 2). However, it has the largest spore size of all *Adiantopsis* taxa (Table 3), it is the only species with 32 spores per sporangium, and it

has indurated pseudoindusia that completely and persistently cover the sori. Two hypotheses may explain these anomalous features. First, the species may be apogamous, a hypothesis supported by the reduced spore number (Evans, 1964; Klekowski, 1973). Alternatively, the spore number may be a function of a reduced number of spore mother cells and a greater resource allocation to fewer spores. Under this hypothesis, the large spores are probably not indicative of a higher ploidy level but rather are an adaptation for limiting spore dispersal. Barrington et al. (1986) observed a similar pattern in *Adiantum pedatum* ssp. *calderi* Cody, a fern that is limited to serpentine rocks. He hypothesized that the large spores may limit spore dispersal and thus prevent them from leaving the “serpentine islands” to which they are adapted. *Adiantopsis asplenioides* appears to fit Barrington et al.’s (1986) model well, as it is a serpentine species with very large spores and based on other features appears to be a diploid. Further, the persistent and indurated pseudoindusia of *A. asplenioides* may represent an additional modification to limit spore dispersal. Thus, the reduced spore number, large spores, and indurated pseudoindusia appear to represent a suite of characters adaptive in keeping propagules within its geographically restricted edaphic niche.

Adiantopsis pedata and *A. pentagona* are hypothesized to be allotetraploid derivatives between *A. radiata* and two different pinnate taxa. A hybrid origin for the pedate Caribbean taxa is supported by the occurrence and morphology of the sterile hybrid *A. ×australopedata* in South America. This taxon documents that the pedate laminar morphology is of hybrid origin between *A. radiata* and a pinnate second parent (Hickey et al., 2003). Also, the dissected echinae bases on spores of *A. radiata* and the pedate taxa support *A. radiata* as one parent, as all other taxa have complete echinae bases. Additional support is evidenced by common laminar development in the two pedate taxa and *A. radiata*. The fronds of young plants, as estimated by rhizome size, are strongly ternate in both species; progressively older, larger plants of these species show increasingly complex frond development. In *A. pedata* the basal basisopic pinnules become extended and the penultimate pinna pairs enlarge, becoming increasingly prominent. In *A. radiata*, additional pinnae pairs are added to the stipe apex. This pattern of growth is only found in *A. radiata*, *A. ×australopedata*, and the pedate Caribbean taxa. The pinnate *Adiantopsis* taxa lack such ontogenetic architectural changes and show a common architecture on both young and old plants.

Adiantopsis reesii is supported as the second parent of *A. pedata* on the basis of crenulate apices

and generally ascending ultimate divisions. Additionally, the carinae of *A. reesii* and *A. pedata* start at stipe bases or in the basal half (*A. pedata*) or quarter (*A. reesii*) of stipes. Both species also share a mode of 14 indurated arcus cells. An *A. reesii* × *A. radiata* origin for *A. pedata* is further supported by the distributions of the taxa, as collections of *A. pedata* are currently only known from areas where the three co-occur.

Numerous morphological comparisons support *Adiantopsis rupicola* as the most likely second parent of *A. pentagona*. The overall ultimate division shape of *A. pentagona* compares most favorably with the generally trullate divisions observed in *Adiantopsis rupicola*. Furthermore, the acute and generally entire ultimate division apices of *A. pentagona* reflect that character state in *A. rupicola*. The generally patent nature of *A. pentagona* ultimate divisions compares favorably with the patent disposition of the ultimate divisions in *A. rupicola*, and both *A. rupicola* and *A. pentagona* have a mode of 16 indurated arcus cells. Finally, the carinae in *A. rupicola* and *A. pentagona* start in the upper portions of stipes (upper 1/3 in *A. pentagona* and 1/4 in *A. rupicola*), a character unique to these two species.

Adiantopsis pentagona, however, is quite variable, and there are suggestions that it may contain yet another cryptic species. Evidence for this comes from some *A. pentagona* specimens that have relatively small ultimate divisions, larger and slightly more compound laminae, and somewhat revolute fertile divisions. It should be noted, however, that all of these character states tend to intergrade across the suite of specimens referable to *A. pentagona*, and it is not clear from this morphological analysis whether the observed variation is due to habitat and ecological differences among plants, simple genetic variation, or multiple origins with different maternal parentages (e.g., *A. rupicola* the maternal parent for some specimens and *A. radiata* for others). Alternatively, *A. pentagona* may be a case of cryptic allotetraploids wherein two distinct species share a common *A. radiata* parent, but each has a different pinnate second parent. The variation in character morphology mentioned above could easily be accounted for if *A. parvisegmenta* was a second parent of some collections. The geographic distribution of specimens does not provide any insight about the source of the morphological variation, and resolution may require molecular analyses. Future molecular studies of this group should encompass the morphological range of *A. pentagona* specimens, *A. rupicola*, *A. parvisegmenta*, and *A. vincentii*, because any one could be a genetic contributor.

TAXONOMY

Adiantopsis Fée, Gen. Filic. [Mém. Foug. 5] 145.

1852. TYPE: *Adiantum pauperculum* Kunze
[= *Adiantopsis paupercula* (Kunze) Fée].

Rhizomes erect, ascending, decumbent, or repent, stiff; *scales* dense, overlapping, persistent, bicolorous with a black, dark brown, or atrocastaneous center and ephemeral, golden or translucent margins, acicular, lanceate, lanceolate, linear, or rarely subulate, basifixed or pseudopeltate, bases truncate or cordate, margins entire, slightly repand, or repand, apices acute, attenuate, acuminate, or cuneate, gland tipped. *Fronde*s aggregated, strict or erect. *Stipes* persistent, atropurpureous, atrocastaneous, or castaneous, always, occasionally, rarely, or never bicarinate adaxially, with scattered pneumatophodes; *carinae* when present, golden; *scales* when present, deciduous, divergent or appressed, concolorous, tan, or bicolorous with broad castaneous to tan center and golden margins, acicular, lanceate, lanceolate, or rarely subulate, pseudopeltate or basifixed, bases biauriculate, truncate, or cordate, margins entire, slightly repand, or repand, apices acute or attenuate, gland tipped; *hairs* diffuse, rare, septate-capitate or rarely ciliform. *Laminae* pinnate, pedate, or palmate, drying brown, green, dull green, dark green, yellow-green, olive-green, or black, apices difform or conform, attenuate, long attenuate, acuminate, acute, or cuneate; *laminar tissue* papyraceous, chartaceous, thin-spongiose, or spongiose, adaxially glabrous with diffuse, glossy-white epidermal cells, hydathodes marginal or in sinuses surrounded by white to pale blue epidermal cells; *hairs* diffuse abaxially, septate-capitate, three celled; *stoma* abaxial, complanate or impressed, anomocytic. *Laminar axes* persistent or marcescent with costae curling acroscopically, atropurpureous, atrocastaneous, or castaneous, grading into lamina and taking its color and texture, or not grading into lamina, adaxially bicarinate; *carinae* golden or colored as axis, interrupted at axis junctions, grading into lamina or not grading into lamina; *scales* when present, concentrated at rachis-costa junctions, diffuse abaxially, deciduous, appressed or patent, concolorous, tan, linear, lanceate, narrowly lanceolate, narrowly rhombic, narrowly triangular, or biseriate, basifixed, bases truncate, acute, or cuneate, margins entire, apices acute or attenuate, gland tipped; *hairs* concentrated at axis junctions, diffuse abaxially, septate-capitate. *Pinnae* ascending, patent, or spreading radially from stipe apex, alternate, sub-opposite, or opposite, incurved in basal half of lamina and straight distally, or straight, narrowly triangular, linear, triangular, narrowly

fusiform, widely rhombic, oblong, or obovate, inequilateral, slightly inequilateral, or equilateral, apices attenuate, acute, or round. *Pinnules* anadromous, slightly ascending, patent, or ascending, linear, narrowly triangular, or narrowly lanceate, apices acute, cuneate, attenuate, or obtuse. *Ultimate divisions* patent, slightly ascending, or ascending, deciduous, articulate or strongly articulate, oblong, narrowly oblong, oblanceolate, obovate, narrowly elliptic, elliptic, flabellate, trullate, lanceolate, ovate, widely rhombiform, or rhombiform, bases cuneate, acute, or truncate, may be uniauriculate acroscopically, margins entire, crenulate, slightly crenulate, or deeply lobed, apices acute, round, or acuminate; *stalks* persistent, may be swollen at junction with laminar tissue. *Veins* free, pseudodichotomous and anadromous or flabellate, immersed or impressed in lamina, occult, obscure, or prominent. *Sori* marginal on both acroscopic and basiscopic margins, uninerved. *Pseudoindusia* distinct or occasionally confluent, lunate, quadrangular, reniform, or subreniform, green to white proximally and hyaline distally, black maculate, hyaline, or white to pale blue, margins slightly erose, entire, or erose. *Sporangia* subglobose to globose, long stalked to sessile. *Spores* 64 or 32 per sporangium, tetrahedral globose, golden or white at maturity, white to pale yellow when immature, echinate or densely echinate with echinae bases complete or dissected, or cristate with anastomosing strands below the muri, laesura obscured by ornamentation or not. *Chromosome number* $2n = 60$ (Walker, 1973; Smith & Foster, 1984).

Generic distribution. The Caribbean and central Mexico to Central America, and through northern South America to northern Argentina (Tryon & Tryon, 1982). For many *Adiantopsis* species, collection data are not clear enough to determine their modern political districts. For collections that indicate an historical political district with insufficient data to determine its modern location, the historical district is included in the specimens examined lists. Collections lacking data to determine a political district at all are indicated as "unknown" in the specimens examined lists.

Nomenclature. Fée (1852) designated *Adiantopsis paupercula* the type species by unambiguously referencing Kunze's 1850 publication of *Adiantum pauperculum*. However, Christensen (1906) later lectotypified the genus with *A. radiata*. Fée's (1852) original typification is recognized as correct here. For more details, see previous discussion in the Taxonomic History section.

Distinguishing characters. *Adiantopsis* is distinguished from *Cheilanthes* by the following combina-

tion of characters: echinate spore ornamentation (excluding *A. asplenioides*); separate and distinct pseudoindusia, each covering a single sorus; an adaxial pair of golden carinae that occur on all laminar axes and generally on stipes, and which are

distinct in color and position from laminar tissue; and finally septate-capitate hairs with distinct, transverse septae and bulbous apical cells, these distributed diffusely on abaxial surfaces of axes and laminar tissue, although often concentrated at axis junctions.

KEY TO THE SPECIES OF CARIBBEAN *ADIANTOPSIS*

- 1a. Lamina palmate 6. *A. radiata*
- 1b. Lamina pedate or pinnate.
 - 2a. Lamina pinnate.
 - 3a. Pseudoindusia indurated with whitened to pale blue cells; sporangia sessile; lamina once pinnate to bipinnate; ultimate divisions deeply lobed 1. *A. asplenioides*
 - 3b. Pseudoindusia not indurated, hyaline to green; sporangia stalked; lamina bipinnate or more compound; ultimate divisions entire to crenulate.
 - 4a. Laminar apex conform; ultimate divisions with stalk swollen at juncture with laminar tissue 3. *A. paupercula*
 - 4b. Laminar apex difform; ultimate divisions without stalk swollen at juncture with laminar tissue.
 - 5a. Lamina quadripinnate; ultimate divisions less than 3.5 mm long and 2.5 mm wide; fertile divisions strongly revolute 2. *A. parvisegmenta* (new species)
 - 5b. Lamina tripinnate or less compound; ultimate divisions more than 3.5 mm long and 2.5 mm wide; fertile divisions more or less flat.
 - 6a. Carinae beginning in upper quarter of stipe; laminar tissue thin-spongiose to chartaceous; mode of 16 indurated arcus cells 8. *A. rupicola*
 - 6b. Carinae beginning at base of or in lower half of stipe; laminar tissue papyraceous; mode of 14 indurated arcus cells.
 - 7a. Apices of ultimate divisions crenulate; rachis basal diameter 1.1–1.5 mm; ultimate divisions ascending; laminar axes persistent, the costae straight; Jamaica and Hispaniola 7. *A. reesii*
 - 7b. Apices of ultimate divisions entire; rachis basal diameter 0.6–1.2 mm; ultimate divisions patent to slightly ascending; laminar axes marcescent, the costae curling acroscopically; Cuba 9. *A. vincentii* (new species)
 - 2b. Lamina pedate.
 - 8a. Apices of ultimate divisions crenulate; carinae beginning in basal half of stipe; mode of 14 annulus cells; ultimate division stalks 0.1–0.6 mm long; ultimate divisions slightly ascending; basal basiscopic pinnules 2.2–5.1 times longer than basal acroscopic pinnule; Jamaica and Hispaniola 4. *A. pedata*
 - 8b. Apices of ultimate divisions acute to round; carinae beginning in apical half of stipe; mode of 16 annulus cells; ultimate division stalks 0.9–6.3 mm long; ultimate divisions more or less patent; basal basiscopic pinnules 1.8–13.1 times longer than basal acroscopic division; Cuba 5. *A. pentagona* (new species)

1. *Adiantopsis asplenioides* Maxon, Amer. Fern J. 22: 14. 1932. TYPE: Cuba. Pinar del Río, Río del Medio, at Las Pozas, very scarce, 10 Sep. 1923, *E. L. Ekman 17456* (holotype, US!). Figure 6A, B.

Rhizome erect, to 1.5 cm long, 0.3–0.8 cm diam.; *scales* bicolorous with an atrocastaneous center and translucent margins, acicular to lanceate (subulate), basifixed, 1.60–5.20 mm long, 0.12–0.55 mm wide, bases truncate, margins entire to slightly repand, apices attenuate. *Fronds* erect, 9.5–18.5 cm long. *Stipes* atrocastaneous to castaneous, never bicarinate adaxially, shorter than lamina, 1.5–4.0 cm long, 0.2–0.6 mm basal diam.; *carinae* absent; *scales* absent; *hairs* rare, septate-capitate or rarely ciliform. *Laminae* pinnate-pinnatifid to bipinnate, linear, drying dull green, 8.0–14.5 cm long, 0.5–1.1 cm wide, apices difform, long attenuate; *laminar tissue* chartaceous, hydathodes marginal in sinuses, surrounded by prominent white to pale blue epidermal cells; *hairs* with basal cell elongate, clear or white, middle cell

short, tan or clear, apical cell elongate-bulbous, clear, white, or golden; *stoma* complanate, guard cells 45.64–57.05 µm long. *Laminar axes* persistent, atrocastaneous to castaneous, grading into lamina and taking its color and texture; *rachis* 0.2–0.5 mm basal diam.; *carinae* colored as axis or golden, grading into lamina; *scales* absent. *Pinnae* patent to slightly ascending, 16–20 pairs, alternate, sub-opposite basally, widely rhombiform, obovate, to oblong, slightly inequilateral to equilateral, to 2.7–6.3 mm long, 1.7–6.0 mm wide, apices round to acute. *Ultimate divisions* patent to slightly ascending, articulate, widely rhombic, flabellate, obovate, to oblong, to 2.6–6.3 mm long, 1.5–6.0 mm wide, bases cuneate, margins deeply 2–6 lobed, apices round to acute; *stalks* persistent, not swollen at junction with laminar tissue, 0.1–0.4 mm long. *Veins* pseudodichotomous, anadromous, immersed in lamina, obscure to occult. *Pseudoindusia* distinct or confluent across sinuses, reniform to sub-reniform, white to pale blue, occasionally hyaline, 0.50–0.78 mm long, 0.36–0.50 mm wide, margin entire to slightly erose. *Sporangia*



Figure 6. —A. *Adiantopsis asplenioides* (Bro. Alain 1226 & Acuna, US). Scale bar = 3.0 cm. —B. Lobed ultimate divisions with indurated pseudoindusia. Scale bar = 0.5 cm. —C. *Adiantopsis parvisegmenta* (C. V. Morton 4166, US). Scale bar = 3 cm. —D. Small, revolute ultimate divisions of *A. parvisegmenta*. Scale bar = 0.15 cm.

globose, sessile on receptacle, arcus of 11–15 indurated cells, these $30.97\text{--}39.12\ \mu\text{m}$ tall. Spores 32 per sporangium, tetrahedral-globose, white to pale yellow at maturity, white to pale yellow when immature, $58.68\text{--}88.02\ \mu\text{m}$ diam., cristate with anastomosing strands below the muri, laesura not obscured by ornamentation. Chromosome number unknown.

Distribution and habitat. A rare endemic of Pinar del Río and an unknown site in eastern Cuba. Restricted to moist, serpentine soils or rocks. In Pinar del Río, Cuba, the species is found on serpentine mogotes. Although there are few collections of this geographically and edaphically restricted taxon, it is likely still extant in Cuba and protected within the confines of Valle de Viñales and other national parks.

Notes. *Adiantopsis asplenioides* is the only Caribbean *Adiantopsis* to possess cristate, rather than echinate, spores. It shares this trait with some putative South American *Adiantopsis*, such as *Cheilanthes dichotoma* Sw. (Ponce & Morbelli, 1989). The ultimate generic position of these cristate taxa will be determined by ongoing research investigating South American *Adiantopsis* and morphologically similar *Cheilanthes*.

Adiantopsis asplenioides is morphologically similar to an undescribed Bolivian and Paraguayan taxon (Barker, pers. obs.). Both taxa have sessile, globose

sporangia, deeply lobed margins, white to pale yellow spores, and prominent white or blue epidermal cells surrounding the hydathodes. These two taxa are distinctive and their relationship with the rest of *Adiantopsis* should be tested with molecular data.

Adiantopsis asplenioides is unique among Caribbean *Adiantopsis* in having 32 large spores per sporangium and indurated pseudoindusia. Although it has the largest spores, this species is likely a diploid, as guard and indurated arcus cell sizes place it among other putative diploid taxa. It is possible that the large spore size and persistent, indurated pseudoindusium are adaptations to restrict spore distribution to the serpentine substrates on which it occurs. The species may also be apogamous, a common cause of reduced spore number.

Selected specimens examined. CUBA. **Pinar del Río:** Loma Zambumbia, Rangel, Sierra del Rosario. Bro. Alain 6108 (US); La Cajalbana, La Palma, Acuña & Alain 15787 (US). **Eastern Cuba:** Cuba Orientali. C. Wright 881 (US).

2. *Adiantopsis parvisegmenta* M. S. Barker & Hickey, sp. nov. TYPE: Cuba. Las Villas (formerly Santa Clara), Trinidad Mtns., Buenos Aires, rare fern on rocks, alt. 800 m. C. V. Morton 4166 (holotype, US!; isotypes, GH!, UC!, US!). Figure 6C, D.

Laminae quadripinnatae; segmenta ultima pusilla, 1.9–3.5 mm longa, 1.2–2.5 mm lata. Ab *A. vincentii* segmentis ultimis fertilis valde revolutis et textura spongiosa differt.

Rhizome ascending to decumbent, to 2.5 cm long, 1.2–2.3 cm diam.; *scales* bicolorous with a black to dark brown center and golden margins, lanceate to acicular, basifixed, 4.50–6.00 mm long, 0.33–0.50 mm wide, bases truncate, margins entire to slightly repand, apices acute. *Fronds* strict, 54.0–74.0 cm long. *Stipes* atrocastaneous, always bicarinate adaxially, shorter than lamina, 15.5–28.3 cm long, 1.6–2.3 mm basal diam.; *carinae* beginning at stipe base or in the basal ¼ of stipe and continuing into rachis; *scales* extending 1.3–3.4 cm up the stipe, divergent, concolorous, tan, lanceolate to acicular (subulate), pseudopeltate to basifixed, 3.40–4.63 mm long, 0.30–0.48 mm wide, bases biauriculate to truncate, margins entire to slightly repand, apices acute; *hairs* rare, septate-capitate. *Laminae* quadripinnate, triangular to lanceate, drying dull green, 26.3–45.7 cm long, 6.5–28.0 cm wide, apices difform, cuneate to acute; *laminar tissue* spongiose, hydathodes marginal; *hairs* with basal cell elongate, clear or white, middle cell short, tan or clear, apical cell bulbous, clear, white, or golden; *stoma* complanate, guard cells 32.60–58.68 µm long. *Laminar axes* persistent, atrocastaneous, grading into lamina and taking its color and texture; *rachis* 1.7–2.3 mm basal diam.; *carinae* golden, grading into lamina; *scales* appressed to patent, narrowly triangular, 0.65–1.10 mm long, 0.02–0.10 mm wide, bases truncate, apices acute. *Pinnae* ascending, 26–45 pairs, alternate, frequently incurved along basal half of lamina, straight distally, triangular to narrowly triangular, inequilateral, to 8.5–16.5 cm long, 3.3–12.5 cm wide, apices acute to cuneate. *Pinnules* patent to slightly ascending, narrowly triangular, to 1.5–7.5 cm long, 0.5–2.5 cm wide, basiscopic pinnules slightly larger than acroscopic pinnules, apices attenuate to cuneate. *Ultimate divisions* patent to slightly ascending, articulate, ovate, elliptic to oblong, 1.9–3.5 mm long, 1.2–2.5 mm wide, bases cuneate, frequently uniauriculate acroscopically, margins entire, apices round to acute; *stalks* persistent, not swollen at junction with laminar tissue, 0.2–0.5 mm long. *Veins* pseudodichotomous, anadromous, immersed in lamina, occult. *Pseudoindusia* distinct, lunate to quadrangular, green to white proximally, hyaline distally, occasionally black maculate, 0.50–0.72 mm long, 0.22–0.48 mm wide, margin erose to slightly erose. *Sporangia* subglobose, long stalked, arcus of (12–)14–25 indurated cells, these 32.60–48.90 µm tall. *Spores* 64 per sporangium, tetrahedral-globose, golden at maturity, white to pale yellow when immature, 34.23–47.27 µm diam., echinate, echinae bases complete,

laesura obscured by ornamentation. *Chromosome number* unknown.

Distribution and habitat. A rare endemic in the Escambray mountains of Cienfuegos, Sancti Spiritus, and Villa Clara Provinces, Cuba. *Adiantopsis parvisegmenta* has been collected on rocks, most likely amphibolite at approximately 800 m altitude. Like other *Adiantopsis* taxa, *A. parvisegmenta* is known from very few collections and from one small geographic region. This species appears to be confined to the amphibolitic substrates of the Escambray Mountains, as it has not been found outside of the region. The Trinidad and Valle de los Ingenios National Park and World Heritage site occur in the range of *A. parvisegmenta* and should afford it some protection.

Notes. As its name implies, *Adiantopsis parvisegmenta* is distinguished from most other pinnate taxa by its small ultimate divisions. However, it may be confused with *A. vincentii*, because the ultimate divisions of the two taxa overlap in size. Three characters can be used to reliably distinguish the two species. *Adiantopsis parvisegmenta* has a spongiose lamina in contrast to the papyraceous lamina of *A. vincentii*. The fertile ultimate divisions of *A. parvisegmenta* are strongly revolute, whereas those of *A. vincentii* are more or less flat. Finally, *A. parvisegmenta* is quadripinnate with a generally broader lamina than *A. vincentii*, which is tripinnate and generally narrower. *Adiantopsis parvisegmenta* is most likely a diploid species, based on indurated arcus cell, guard cell, and spore sizes, and may contribute to the parentage of some elements of the putative allotetraploid *A. pentagona*.

It should be noted that specimens of *Adiantopsis parvisegmenta* were frequently determined as *A. reesii*. In folders at US, Proctor noted that these collections were not *A. reesii*, and he was correct. Thus, Cuban material determined as *A. reesii* may be *A. parvisegmenta*, *A. rupicola*, or *A. vincentii*, as these species were frequently included under *A. reesii* by past researchers.

Paratypes. CUBA. **Las Villas:** Las Lagunas, Buenos Aires, J. G. Jack 6869 (NY), 6877 (US), 7033 (US [2]).

3. *Adiantopsis paupercula* (Kunze) Fée, Gen. Filic. [Mém. Foug. 5]: 145. 1852. *Adiantum pauperculum* Kunze, Farrnkräuter 2(13): 65. t. 127. 1850. *Cheilanthes paupercula* (Kunze) Mett., Fil. Hort. Bot. Lips. 52. 1856. *Hypolepis paupercula* (Kunze) Hook., Sp. Fil. 2: 73. t. 88-C. 1856. TYPE: Cuba. Oriente, Mt. Líbano, 1844, J. Linden 1864 (holotype, LZ not seen; isotypes,

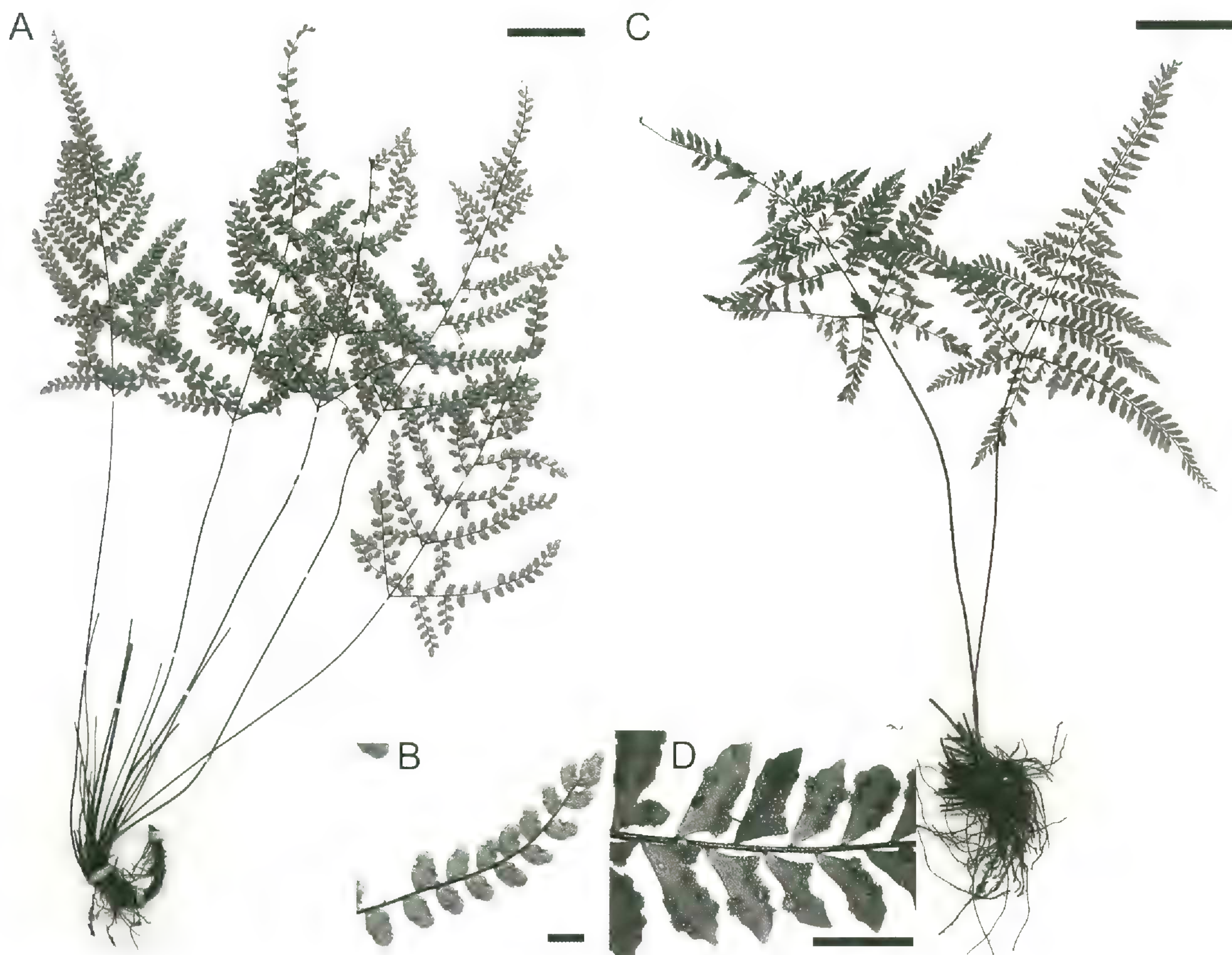


Figure 7. —A. *Adiantopsis paupercula* (W. R. Maxon 4239, US). Scale bar = 3 cm. —B. Ultimate divisions of *A. paupercula*. Scale bar = 0.5 cm. —C. *Adiantopsis pedata* (Wm. Harris 10878, GH). Scale bar = 3 cm. —D. Ultimate divisions of *A. pedata* with toothed apices. Scale bar = 0.75 cm.

BI, BM!, BM photo US!, K!, L!, P!, US!).
Figure 7A, B.

Rhizome decumbent to erect, to 5.9 cm long, 0.3–1.1 cm diam.; *scales* bicolorous with a black to dark brown center and golden margins, lanceate to acicular, basifixed, 3.61–13.93 mm long, 0.30–0.87 mm wide, bases truncate, margins entire, apices attenuate. *Fronds* erect, 12.5–65.5 cm long. *Stipes* atropurpureous to atrocastaneous, always bicarinate adaxially, longer than or equal (shorter) to lamina, 8.5–35.5 cm long, 0.4–2.3 mm basal diam.; *carinae* beginning near midpoint of stipe and continuing into rachis; *scales* extending 1.4–6.4 cm up the stipe, divergent, concolorous, tan, lanceate, pseudopeltate to basifixed, 3.2–9.5 mm long, 1.2–5.2 mm wide, bases biauriculate to truncate, margins entire, apices attenuate; *hairs* septate-capitate. *Laminae* tripinnate, bipinnate, to quadripinnate, triangular, drying green to brown, 9.5–30.0 cm long, 4.5–19.0 cm wide, apices conform, attenuate; *laminar tissue* spongy, hydathodes marginal; *hairs* with basal cell elongate, clear or white, middle cell short, clear, red, or golden,

apical cell bulbous, clear, red, or golden; *stoma* complanate, guard cells 48.90–68.46 μm long. *Laminar axes* persistent, atropurpureous to atrocastaneous, not grading into lamina at apices; *rachis* 0.5–1.4 mm basal diam.; *carinae* golden, not grading into lamina; *scales* absent. *Pinnae* ascending to patent, 21–33 pairs, alternate, occasionally incurved in basal half of lamina, straight distally, linear to narrowly triangular, inequilateral, to 3.1–12.4 cm long, 0.9–7.4 cm wide, apices acute to cuneate. *Pinnules* slightly ascending to patent, linear, basal pinnules 1.1–6.0 cm long, 0.5–1.0 cm wide, basiscopic pinnules slightly larger than acroscopic pinnules, apices cuneate to acute. *Ultimate divisions* slightly ascending to patent, strongly articulate, flabellate, rhombiform, to oblong, 3.2–8.0 mm long, 2.5–4.5 mm wide, bases acute to truncate, margins entire, apices round to acute; *stalks* persistent, swollen at junction with laminar tissue, 2.4–1.8 mm long. *Veins* flabellate, immersed in lamina, occult to obscure. *Pseudoindusia* distinct, lunate, hyaline, occasionally black maculate, 0.8–0.9 mm long, 0.25–0.60 mm wide, margin erose. *Sporangia* subglobose, long stalked, arcus of 14–20 indurated

cells, these 35.86–47.27 μm tall. Spores 64 per sporangium, tetrahedral-globose, golden at maturity, white to pale yellow when immature, 35.86–45.64 μm diam., echinate, echinae compact with complete bases, laesura obscured by ornamentation. *Chromosome number* unknown.

Distribution and habitat. Found on the islands of Cuba, Jamaica, and Puerto Rico on shaded, rocky limestone or serpentine slopes and cliffs between 400–1000 m altitude. *Adiantopsis paupercula* is the most widespread endemic Caribbean *Adiantopsis*. This is probably because the species can occur on both limestone and serpentine substrates, whereas other endemic Caribbean *Adiantopsis* appear to have greater substrate specificity. It should be noted that on two recent collecting trips to Puerto Rico *A. paupercula* was not found, and it may no longer be on the island, because it was previously known from only one collection (Proctor, 1989). However, it probably still occurs on Cuba and Jamaica. In Cuba, some of its habitat is protected by the Alejandro de Humboldt National Park and World Heritage site.

Notes. *Adiantopsis paupercula* is one of the more distinctive *Adiantopsis* species. The strongly articulate, flabellate to rhombiform ultimate divisions with a swelling at the junction of the stalk and laminar tissue distinguish this species from other *Adiantopsis*. It is likely a diploid species, because its indurated arcus cell and spore sizes place it within a diploid group of taxa. However, its guard cell sizes are larger than other putative diploids, and it is not clear why.

Selected specimens examined. CUBA. **Guantanamo:** Top of El Yunque, limestone mtn. near Baracoa, *E. L. Ekman* 3977 (US); Monte Libanon, San Fernandez, *E. L. Ekman* 10308 (B, US). **Holguin:** Mina Cayoguan, *Bro. Clement* 3982 (US); Vedado-Habana, Banks of Cayoguan River N of Sierra de Moa, *Fres Lein* 20910, *M. Victorin, Clement* (US); Sierra de Nipe, headwaters of Pilots River, *E. L. Ekman* 2515 (B, BM, US); Camp La Gloria, S of Sierra Moa, *J. A. Shafer* 8174 (K, US); Sierra Nipe, near Woodfred, Rocky Arroyos, *J. A. Shafer* 3169 (K, MO, US); Sierra de Nipe, Loma Monsura, NW side of top, *E. L. Ekman* 5746 (US); Sierra Nipe, along Rio Medio near Woodfred, *C. V. Morton* 4526, *Julian Acuna* (US); Vedado Habana, Pena Prieta, *Bro. Alain* 3583 (US). **Oriente:** Mt. Libano, *J. Linden* 1862 (K); Monte Libano, caverns of Thermopylae & vic., *W. R. Maxon* 4239 (P, US [2]); Monte Verde, *C. Wright* 962 (UC); Monte Verde, *C. Wright* 964 (BM [2], K [3], L, MO, US [3]).

JAMAICA. **Clarendon:** Peckham Woods, *W. Harris* 11021 (BM, US); Peckham Woods, *W. Harris* 12771 (BM, K [2], MO, US); Peckham Woods, *W. T. Stearn* 17 (BM). **Portland:** E slope of John Crow Mtns. ca. 2.5 mi. SW of Ecclesdown, *G. R. Proctor* 5729 (MO). **St. Ann:** Douglas Castle District, ca. 2 mi. NW of Mason River Savanna, *A. M. Evans* 2349 (BM). **Trelawny:** On limestone cliffs, *L. M. Underwood* 3304 (US, P); Six mi. WNW of Troy on Crown Lands Road, *H. A. Hespenheide* 1191, *E. B. Hespenseide, J. S. Calver, R. E. Ricklefs* (DUKE, UC, US); Crown Lands Road extension ca. 5 mi. NW of Troy, *G. R. Proctor* 31099 (DUKE);

4 mi. WNW of Troy on Crown Lands Road, *H. A. Hespenheide* 1180 (DUKE); On limestone rocks, *L. M. Underwood* 3303 (US); Near Troy, *W. Harris* 8791 (BM).

PUERTO RICO. **Maricao:** Maricao State Forest, Barrio Tabonuco, headwaters stream of Rio Seco, below Road 120, km. 10.15, *G. R. Proctor* 41649 (US).

4. *Adiantopsis pedata* (Hook.) T. Moore, Ind. Fil. 18. 1857. *Hypolepis pedata* Hook., Sp. Fil. 2: 73, t. 92-A. 1852. *Cheilanthes pedata* (Hook.) A. Braun, Index Seminum. 1857. TYPE: Jamaica. *Purdie s.n.* (holotype, K!, K photo B!, K photo MICH!; isotypes, BM!, BM photo B!, BM photo MICH!, P!). Figure 7C, D.

Rhizome erect to decumbent, to 3.0 cm long, 0.6–1.4 cm diam.; *scales* bicolorous with a black to dark brown center and golden margins, lanceate, basifixed, 3.50–4.75 mm long, 0.43–0.45 mm wide, bases truncate, margins entire, apices acute. *Fronde* strict, 21.7–32.3 cm long. *Stipes* atropurpureous to atrocastaneous, always bicarinate adaxially, longer than or equal to lamina, 11.3–19.0 cm long, 0.8–1.3 mm basal diam.; *carinae* beginning at stipe base or in the basal $\frac{1}{2}$ of stipe and continuing into rachis; *scales* extending 2.3–3.4 cm up the stipe, appressed, concolorous, tan, lanceolate, pseudopeltate, 3.50–4.00 mm long, 0.53–0.58 mm wide, bases biauriculate, margins entire to slightly repand, apices acute; *hairs* rare, septate-capitate. *Laminae* pedate, tripinnate to rarely quadripinnate basally, abruptly bipinnate above, broadly deltate-pentagonal, drying yellow-green, green, dark green to brown, 8.5–19.4 cm long, 9.4–25.7 cm wide, apices difform, attenuate; *laminar tissue* chartaceous, hydathodes marginal; *hairs* with basal cell elongate and clear, middle cell frequently short and red, golden red, golden, or white, apical cell bulbous and clear, white, or golden; *stoma* complanate, guard cells 53.79–78.24 μm long. *Laminar axes* persistent, atropurpureous to atrocastaneous, grading into lamina and taking its color and texture; *rachis* 0.4–1.0 mm basal diam.; *carinae* golden, grading into lamina; *scales* appressed to patent, linear, 0.45–0.88 mm long, 0.02–0.07 mm wide, bases truncate, apices acute. *Pinnae* ascending to patent, 21–28 pairs, basal pinnae opposite to subopposite, straight, triangular, inequilateral, to 4.7–12.9 cm long, 1.7–6.0 cm wide, apices attenuate to acute; penultimate pinnae opposite to subopposite, narrowly fusiform to linear, abruptly shorter, 2.5–7.1 cm long; distal pinnae alternate, quickly reduced in length. *Pinnules* patent to slightly ascending, linear, apices attenuate to cuneate; *basal basisopic pinnules* of basal pinnae narrowly triangular to fusiform, much extended, 1.0–5.6 cm long, 2.2–5.1 times longer than basal acroscopic pinnule, basal

acroscopic pinnule 0.5–1.3 cm long, distal pinnules of first pinnae equivalent, abruptly shorter than basal basiscopic pinnule. *Ultimate divisions* ascending, articulate, oblanceolate, narrowly elliptic, to narrowly oblong, 4.0–9.0 mm long, 1.4–3.5 mm wide, bases cuneate, uniauriculate acroscopically, margins entire proximally, crenulate distally, apices round to acute; *stalks* persistent, not swollen at junction with laminar tissue, 0.10–0.60 mm long. *Veins* pseudodichotomous, anadromous, immersed in lamina, occult to obscure. *Pseudoindusia* distinct, lunate to quadrangular, green to white proximally, hyaline distally, occasionally black maculate, 0.60–0.84 mm long, 0.30–0.56 mm wide, margin slightly erose. *Sporangia* subglobose, long stalked, arcus of 13–15(–20) indurated cells, these 40.75–55.42 μm tall. *Spores* 64 per sporangium, tetrahedral-globose, golden at maturity, white to pale yellow when immature, 38.31–54.61 μm diam., densely echinate, echinae bases dissected, laesura obscured by ornamentation. *Chromosome number* unknown.

Distribution and habitat. *Adiantopsis pedata* is a rare fern known only from the Dominican Republic and Jamaica. The species has been collected in humus on wooded hillsides scattered with limestone rocks at 800–1000 m altitude. Although no recent collections have been made, it occurs in very rural areas that have relatively little economic development, such as the Cockpit Country of Jamaica. Given that ecotourism is becoming an industry in this part of Jamaica, the habitat of *A. pedata* is likely to be preserved, and the species may still be found there if collections are sought.

Notes. *Adiantopsis pedata* formerly included plants from Cuba. However, the Cuban material recognized here as *A. pentagona* is clearly distinct. Carinae beginning in the basal half of the stipes, generally ascending ultimate divisions with crenulate apices, and a mode of 14 indurated arcus cells distinguish *A. pedata*. *Adiantopsis pentagona* has carinae beginning in the apical half of the stipes, patent or slightly ascending ultimate divisions, entire or only slightly crenulate ultimate division apices, and a mode of 16 indurated arcus cells. Both Caribbean taxa may be confused with the South American *A. ×australopedata*, which is a sterile hybrid that occurs in the tri-border region of Argentina, Brazil, and Paraguay. The aborted spores, crenulate margins, and generally much larger frond size distinguish *A. ×australopedata* from the Caribbean taxa (Hickey et al., 2003).

Adiantopsis pedata appears to be a tetraploid derivative of *A. radiata* and *A. reesii*. Indurated arcus cell, guard cell, and spore sizes strongly suggest that it

is tetraploid. Its pedate morphology suggests that it is a hybrid taxon, with *A. radiata* as one parent (Hickey et al., 2003). Also shared with *A. radiata* are spore echinae that are basally dissected, and a common pattern of laminar development. With *A. reesii*, *A. pedata* shares distinctly toothed ultimate division apices, a mode of 14 indurated arcus cells, and carinae beginning in the lower portions of the stipe. Based on all these data, *A. pedata* is supported as a tetraploid derivative of *A. radiata* and *A. reesii*. Future cytological research needs to be conducted to confirm its ploidy level, and future molecular research should test the parentage of *A. pedata*.

Selected specimens examined. DOMINICAN REPUBLIC. **Monte Cristi:** Cordillera Central, Monción. *E. L. Ekman* 12693 (B, BM, K, US [2]).

JAMAICA. **Clarendon:** Peckham Woodland, *W. Harris* 10,878 (B, GH, K, US [2]); Glenwood Springs, along road between Balcarres & Sunbury, *G. R. Proctor* 35655 (US). **Unknown Parish:** Jamaica, *Walker-Arnott s.n.* (NY).

5. *Adiantopsis pentagona* M. S. Barker & Hickey, sp. nov. TYPE: Cuba. Santa Clara, vic. of Sopapo, Buenos Aires, Trinidad Mtns., shaded limestone cliff, 4 Aug. 1936, *L. B. Smith* 3320, *A. R. Hodgdon*, & *F. Gonzalez* (holotype, GH!; isotypes, NY!, US!). Figure 8A, B.

Laminae pedatae; pinnae supernae bipinnatae; pinnae basales tripinnatae, pinnulis valde basalibus elongatis magnopere. Ab *A. pedata* carinis in dimidio superno stipitis exorientibus, segmentis ultimis patentibus vel leviter ascendentibus praebentibus apices integros vel leviter crenulatos, arcu e cellulis induratis 16 (modus) composito, et ab *A. ×australopedata* sporis fertilibus (nonabortivis) differt.

Rhizome erect to decumbent, to 3.8 cm long, 0.5–1.8 cm diam.; *scales* bicolorous with a black to dark brown center and golden margins, acicular to lanceate, basifixed, 2.13–7.58 mm long, 0.08–0.88 mm wide, bases truncate, margins repand to entire, apices acute. *Fronds* strict, 33.2–72.1 cm long. *Stipes* atropurpureous to atrocastaneous, always bicarinate adaxially, longer than or equal to lamina, 17.1–44.0 cm long, 0.8–2.1 mm basal diam.; *carinae* beginning in the upper $\frac{1}{3}$ ($\frac{1}{2}$) of stipe and continuing into rachis; *scales* extending 2.0–3.7 cm up the stipe, appressed, concolorous, tan, acicular to lanceate (subulate), pseudopeltate, 1.05–6.38 mm long, 0.13–0.83 mm wide, bases biauriculate, margins entire to slightly repand, apices acute; *hairs* rare, septate-capitate. *Laminae* pedate, tripinnate to quadripinnate basally, abruptly bipinnate above, broadly deltate-pentagonal, drying brown, dark green, green to yellow-green, 14.7–28.1 cm long, 12.8–48.2 cm wide, apices difform, long attenuate; *laminar tissue* thin-spongiose,

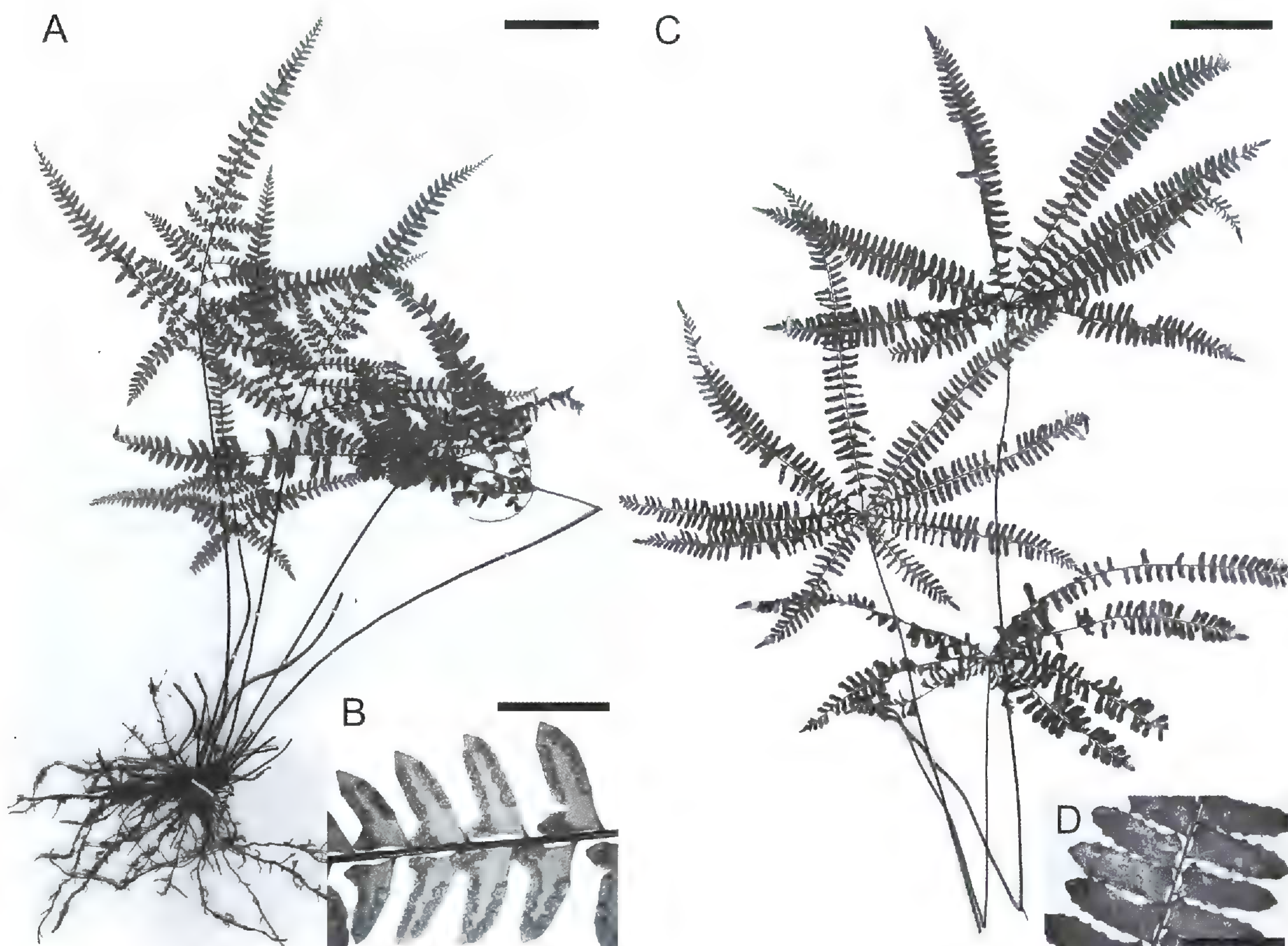


Figure 8. —A. *Adiantopsis pentagona* (J. B. Smith 3320 et al., US). Scale bar = 3 cm. —B. Ultimate divisions of *A. pentagona* without toothed apices. Scale bar = 0.75 cm. —C. *Adiantopsis radiata* (G. R. Proctor 29256, F). Scale bar = 3 cm. —D. Ultimate divisions of *A. radiata*. Scale bar = 0.75 cm.

hydathodes marginal; *hairs* with basal cell elongate and clear, middle cell frequently short and white, golden, golden red, or red, apical cell bulbous and clear, white, or golden; *stoma* complanate, guard cells 48.90–83.13 μm long. *Laminar axes* persistent, atropurpureous to atrocastaneous, grading into lamina and taking its color and texture; *rachis* 0.5–1.3 mm basal diam.; *carinae* golden, grading into lamina; *scales* appressed to patent, lanceate to linear, 0.77–1.45 mm long, 0.08–0.17 mm wide, bases truncate, apices attenuate. *Pinnae* patent to ascending, 28–40 pairs, basal pinnae opposite to sub-opposite, straight, triangular, inequilateral, to 6.4–24.1 cm long, 2.8–19.9 cm wide, apices attenuate to acute; penultimate pinnae sub-opposite, linear, abruptly shorter, 1.4–14.2 cm long; distal pinnae alternate, quickly reduced in length. *Pinnules* patent to slightly ascending, linear to narrowly lanceate, apices cuneate to attenuate; *basal basiscopic pinnules* of basal pinnae fusiform to narrowly triangular, much extended, 1.8–15.3 cm long, 1.8–13.1 times longer than basal acroscopic pinnule, basal acroscopic pinnule 0.4–5.8 cm long, distal pinnules of first pinnae equivalent, abruptly shorter than basal basiscopic pinnule. *Ultimate*

divisions patent to slightly ascending, articulate, narrowly oblong, oblanceolate, lanceolate, to narrowly elliptic, 6.1–11.1 mm long, 2.5–4.2 mm wide, bases cuneate, frequently uniauriculate acroscopically, margins entire to slightly crenulate, apices round to acute; *stalks* persistent, not swollen at junction with laminar tissue, 0.9–6.3 mm long. *Veins* pseudodichotomous, anadromous, immersed in lamina, occult to obscure. *Pseudoindusia* distinct, lunate to quadrangular, hyaline with a brown or black area proximally where hydathode terminates, occasionally black maculate, 0.35–1.10 mm long, 0.20–0.60 mm wide, margin entire to slightly erose. *Sporangia* subglobose, long stalked, arcus of 14–22 indurated cells, these 40.75–58.68 μm tall. *Spores* 64 per sporangium, tetrahedral-globose, golden at maturity, white to pale yellow when immature, 40.75–58.90 μm diam., densely echinate, echinae bases dissected, laesura obscured by ornamentation. *Chromosome number* unknown.

Distribution and habitat. A Cuban endemic found in the province of Pinar del Río, and the Escambray Mountains of Cienfuegos, Sancti Spiritus, and Villa Clara. *Adiantopsis pentagona* has been collected on moist, shaded limestone or amphibolite soils, rocks,

cliffs, and cave entrances. When *A. pentagona* has been collected in soil, it was generally found on slopes scattered with limestone or amphibolite rocks. *Adiantopsis pentagona* is most likely still found in Cuba. In Pinar del Río, it is probably protected within the boundaries of Valle de Viñales National Park, and by the Trinidad and Valle de los Ingenios National Park in the Escambray Mountains.

Notes. *Adiantopsis pentagona* is named for the overall pentagonal outline of the lamina. *Adiantopsis pedata* and *A. ×australopedata* also have pentagonal laminar outlines and may be confused with *A. pentagona*. Carinae beginning in the basal half of the stipes, distinctly crenulate ultimate division apices, generally ascending ultimate divisions, and mode of 14 indurated arcus cells, distinguish *A. pedata* from *A. pentagona*, which has carinae beginning in the apical half of the stipe, entire or slightly crenulate ultimate division apices, patent to slightly ascending ultimate divisions, and a mode of 16 indurated arcus cells. *Adiantopsis ×australopedata*, a hybrid distributed in the tri-border region of Argentina, Brazil, and Paraguay, may be distinguished from the Caribbean species by its aborted spores, crenulate margins, and generally larger laminae.

Adiantopsis pentagona appears to be the allotetraploid derivative of *A. radiata* and *A. rupicola*. The large spores, guard cells, and indurated arcus cells relative to putative diploid taxa, such as *A. radiata* and *A. rupicola*, suggest that *A. pentagona* is a tetraploid. Its pedate morphology suggests that it is a hybrid taxon, with *A. radiata* as one parent (Hickey et al., 2003). Also shared with *A. radiata* are spore echinae that are basally dissected, and a common pattern of laminar development. With *A. rupicola*, *A. pentagona* shares carinae beginning in the apical portion of stipes, a mode of 16 indurated arcus cells, and the overall ultimate division shape agrees most favorably with *A. rupicola*. The type of *A. pentagona*, *Smith 3320 et al.*, was selected in part because its morphology supports an allotetraploid origin involving *A. radiata* and *A. rupicola*. However, some collections of *A. pentagona*, specifically those with relatively small ultimate divisions that are revolute when fertile suggest that *A. parvisegmenta* may be the parent of a second, cryptic species. This putative cryptic species has been retained in *A. pentagona* because the available data do not clearly differentiate it. Future molecular research should encompass the morphological range of *A. pentagona* and include *A. rupicola*, *A. parvisegmenta*, and *A. vincentii*, to evaluate if cryptic elements are included.

Paratypes. CUBA. **Las Villas:** Las Vegas de Matagua, Trinidad Mtns., *C. V. Morton 10547* (DUKE, US), *C. V. Morton 10799* (BM, DUKE, US [2]); Las Vegas de Matagua,

Buenos Aires, *J. G. Jack 7903* (GH [2], NY, US); On the crest of Pico Petrerillo, Trinidad Mtns., *Bro. Alain 6715* (MICH, US); Buenos Aires, Trinidad Mtns., *C. V. Morton 4179* (GH, UC, US); Sierra del Bibisial, Loma de Ponciano, Sancti-Spiritus Mtns., *F. Leon 6712*, *F. Clement* (NY); San Blas-Buenos Aires, Trinidad Mtns., gulley behind Gavinas, *R. A. Howard 6505* (GH, MO); Trinidad Mtns., *Glen Ames 11, 173* (MICH); Deep limestone cave near San Jose, *R. A. Howard 5154* (GH, MO, NY [2]); Buenos Aires, *Roig 6124*, *Acuna* (NY); Hanabanilla Falls, *R. Howard 146*, *W. Briggs*, *P. Kamb*, *I. Lane*, *R. Ritland* (GH); San Blas, Naranjal, Trinidad Mtns., *R. A. Howard 5387* (GH, MO, NY); Pitajones, *J. A. Shaffer 12204* (GH [2], NY); San Blas-Buenos Aires, Trinidad Mtns., roadsides near Mina Carlota, *A. Gonzales 513* (BM, GH, US); San Blas-Buenos Aires, Trinidad Mtns., Gavinas, *R. A. Howard 6539* (GH); Las Lagunas, Buenos Aires, *J. G. Jack 6869* (US); Buenos Aires, Trinidad Hills, *J. G. Jack 7773* (US). **Pinar del Río:** Sierra de las Animas, *E. L. Ekman 10510* (NY, US). **Sancti Spiritus:** Mogote Caburni, *P. Acevedo-Rdgz.*, 6461 *R. Oviedo*, *M. Fernandez*, *N. Vera* (US). **Unknown Province:** *C. Wright 3947* (B); *C. Wright 3949* (GH, K, NY [2]); 1867, c. l. bos. Desd. s.n. (FI).

6. *Adiantopsis radiata* (L.) Fée, Gen. Filic. [Mém. Foug. 5]: 145. 1852. *Adiantum radiatum* L., Sp. Pl. 2: 1094. 1753. *Cheilanthes radiata* (L.) John. Smith, J. Bot. (Hooker) 4: 159. 1841. *Hypolepis radiata* (L.) Hook., Sp. Fil. 2: 72. 1852. TYPE: *Sloane "Adiant. 3 radiatum"* (lectotype, LINN 1252.1, chosen by Lellinger, Mem. New York Bot. Gard. 23: 3. 1972). Figure 8C, D.

Rhizome erect, to 3.3 cm long, 0.5–0.9 cm diam.; **scales** bicolorous with a black to dark brown center and golden margins, lanceolate to acicular, pseudopeltate to basifixed, 3.75–4.43 mm long, 0.41–0.58 mm wide, bases cordate to truncate, margins repand, apices acute to acuminate. **Fronds** strict, 19.7–62.3 cm long. **Stipes** atropurpureous to atrocastaneous, rarely bicarinate adaxially, longer than lamina, 10.5–47.0 cm long, 0.8–2.0 mm basal diam.; **carinae** when present, beginning at stipe base and continuing into lamina; **scales** extending 0.2–3.5 cm up the stipe, appressed, bicolorous with broad castaneous to tan center and golden margins, or concolorous, tan, lanceolate, pseudopeltate, 3.00–5.50 mm long, 0.45–0.75 mm wide, bases biauriculate, margins repand, apices acute; **hairs** rare, septate-capitate. **Laminae** palmate, radially bipinnate, orbiculate, geniculate, drying olive-green, dark green, black, to yellow green, 10.2–26.3 cm long, 4.4–25.8 cm wide, apices difform, acute; **laminar tissue** thin-spongiose, hydathodes marginal; **hairs** with basal cell elongate and clear, middle cell frequently short and golden or red, apical cell bulbous and clear or white; **stoma** complanate, guard cells 35.86–63.57 µm long. **Laminar axes** persistent, atropurpureous to atrocastaneous, grading into lamina and taking its color and texture; **carinae** golden, grading into lamina;

scales absent. *Pinnae* spreading radially from stipe apex, 3–9, straight, linear to narrowly fusiform, apices acute; central pinna to 9.2–15.3 cm long, 1.4–2.7 cm wide; basal pinna to 2.6–9.2 cm long, 1.0–2.2 cm wide; *basal flabellate divisions* often fertile, attached to the stipe apex between pinnae. *Ultimate divisions* patent to ascending, articulate, oblong to narrowly oblong, 6.0–13.5 mm long, 2.1–3.7 mm wide, bases cuneate to acute, margins entire to crenulate, apices round to acute; *stalks* persistent, not swollen at junction with laminar tissue, 1.0–6.0 mm long. *Veins* pseudodichotomous, anadromous, immersed in lamina, obscure to occult. *Pseudoindusia* distinct, lunate to quadrangular, hyaline, occasionally black maculate, 0.4–0.84 mm long, 0.22–0.56 mm wide, margin entire to slightly erose. *Sporangia* subglobose, long stalked, arcus of 16–27 indurated cells, these 30.97–46.46 µm tall. *Spores* 64 per sporangium, tetrahedral-globose, golden at maturity, white to pale yellow when immature, 34.23–47.27 µm diam., densely echinate, echinae bases dissected, laesura obscured by ornamentation. *Chromosome number* $n = 30$.

Distribution and habitat. *Adiantopsis radiata* is by far the most common and widely distributed *Adiantopsis* species. The species is widespread throughout tropical America and occurs from the Caribbean and Mexico south to Argentina. It has most often been collected on moist, calcareous or serpentine, rocky, wooded slopes and has also been collected on limestone cliffs and walls.

Notes. *Adiantopsis radiata* is the most distinctive *Adiantopsis* species, as it is the only palmate species. As the name implies, the pinnae radiate outward from a single point at the stipe apex. Young *A. radiata* may be confused with young *A. pedata* and *A. pentagona* because all three taxa share a similar ternate juvenile form. The most reliable character to distinguish these taxa is indurated arcus cell number. *Adiantopsis radiata* has a mode of 20 indurated arcus cells, whereas *A. pedata* possesses a mode of 14 and *A. pentagona* has a mode of 16. Also, the stipes of *A. radiata* are typically lacking carinae, whereas both *A. pedata* and *A. pentagona* stipes are always adaxially bicarinate. Another character that is useful for distinguishing *A. radiata* and *A. pedata* is ultimate division shape and orientation. The ultimate divisions of *A. radiata* are usually oblong with rounded apices and are generally patent. *Adiantopsis pedata* ultimate divisions are more frequently oblanceolate with a distinctly toothed apex and are ascending.

Adiantopsis radiata is implicated in an interesting pattern of reticulate and morphological evolution. The species apparently hybridizes with various pinnate taxa to produce pedate derivatives. In the Caribbean,

these hybrid derived pedate taxa are *A. pedata* and *A. pentagona*, and in South America *A. ×australopedata* (Hickey et al., 2003).

Selected specimens examined. CUBA. **Oriente:** Deciduous woods near base of Loma Menqura, *J. A. Shafer* 3777 (F); Monte Verde, *C. Wright* 963 (F, MO [2]). **Unknown province:** 1889, *Eggers* 4813 (F).

JAMAICA. **Clarendon:** Peckham Woods, *G. R. Proctor* 8445 (MO); Peckham Woodland, *W. Harris* 10860 (F); Summit area of Crofts Mtn., *G. R. Proctor* 29256 (F). **Portland:** 1906, *A. Moore* (MICH). **Trelawny:** Vic. of Troy, *W. R. Maxon* 2954 (MICH). **Unknown Parish:** 1886, *J. P.* 390 (MO); *W. Harris* 9163 (MO).

LESSER ANTILLES. **Dominica:** Cliffs in woodlands on the North River watershed, W slopes of Morne Brule, Portsmouth, *W. H. Hodge* 72 (MO [2]); St. Paul, Morne Cola Anglais, *G. L. Webster* 13425 (MICH, MO). **Martinique:** 1868, *Sidier s.n.* (F). **Montserrat:** Cudjor Lerad, *J. A. Shafer* 453 (F). **Guadeloupe:** Falaises de la rivière des Pères, *Blanchau s.n.* (F). **Unknown Island:** 1881, *J. L. Main s.n.* (MU).

TRINIDAD. 1877–1878, *A. Fendler* 7 [herb. chas. *H. Ford* 1354] (F, MICH, MO); Blanchissense Road near Verdant Vale on Banks Main Road, *A. Hambersley s.n.* (F).

7. *Adiantopsis reesii* (Jenm.) C. Chr., Ind. Fil. 22. 1905. *Cheilanthes reesii* Jenm., J. Bot. Brit. For. 24: 267. 1886. TYPE: Jamaica. St. Elizabeth Parish, Oxford, *Rev. T. L. Rees s.n.* (holotype, K!, K photo US!; isotype, BM!, BM photo US!). Figure 9A, B.

Rhizome decumbent to ascending, to 2.8 cm long, 0.6–0.8 cm diam.; *scales* bicolorous with a black to dark brown center and golden margins, lanceate to acicular, basifixed, 4.05–5.50 mm long, 0.52–0.61 mm wide, bases truncate, margins slightly repand, apices acute. *Fronde* strict, 17.1–60.0 cm long. *Stipes* atrocastaneous, always bicarinate adaxially, much shorter than lamina, 2.2–22.0 cm long, 1.0–2.6 mm basal diam.; *carinae* beginning at stipe base or in the basal ¼ of stipe and continuing into rachis; *scales* extending 1.9–4.2 cm up the stipe or to the rachis, divergent, concolorous, tan, lanceate to acicular (subulate), pseudopeltate, 1.25–5.75 mm long, 0.20–0.74 mm wide, bases cordate, margins entire to slightly repand, apices acute; *hairs* rare, septate-capitate. *Laminae* tripinnate, lanceolate to narrowly triangular, drying dull green, 5.0–53.0 cm long, 5.5–14.6 cm wide, apices difform, attenuate to acuminate; *laminar tissue* papyraceous, hydathodes marginal; *hairs* with basal cell elongate and clear, middle cell frequently short and clear, brown, or red, apical cell bulbous and frequently covering middle cell, white, clear, or golden; *stoma* impressed, guard cells 32.60–53.79 µm long. *Laminar axes* persistent, atrocastaneous, grading into lamina and taking its

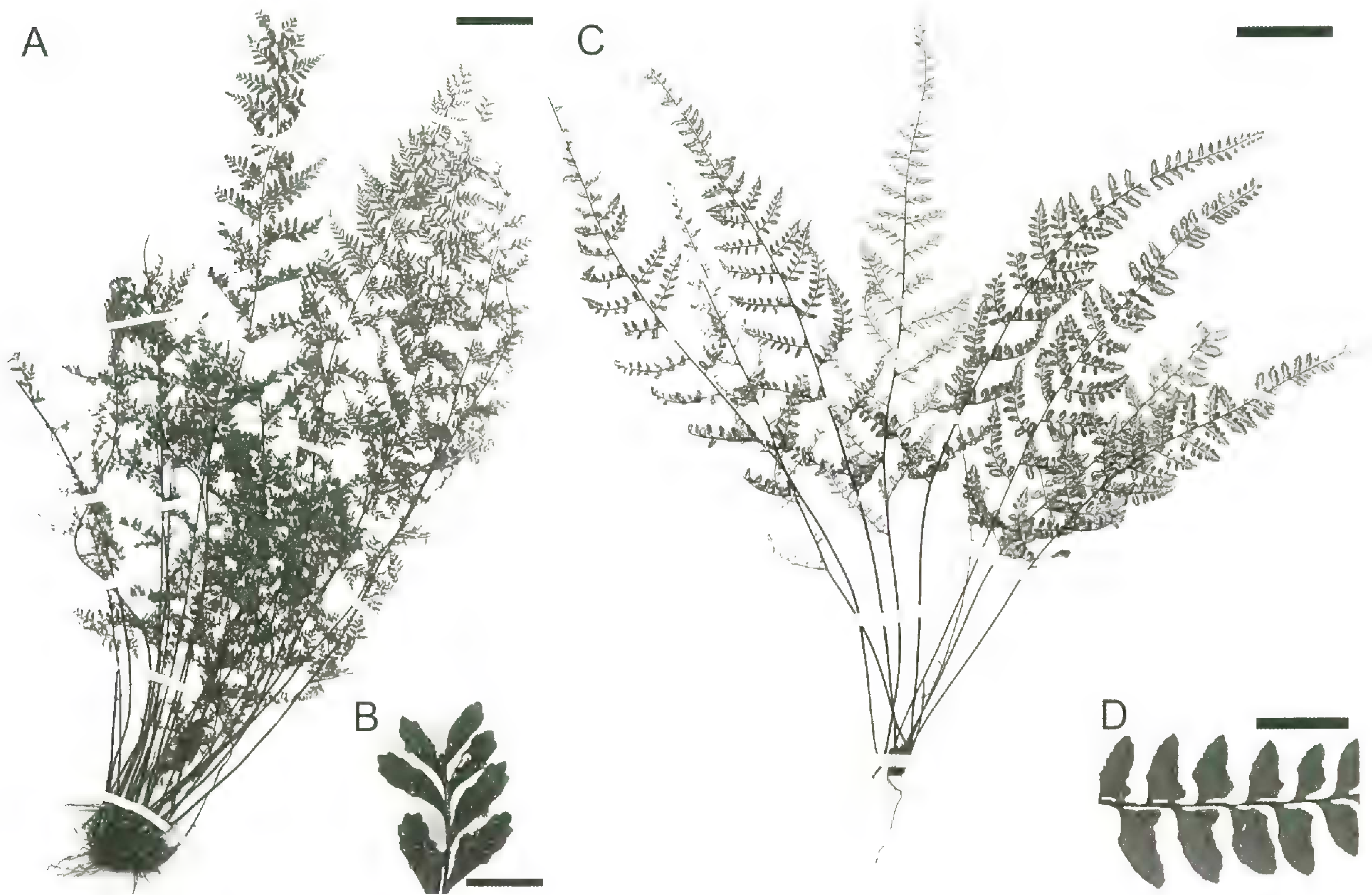


Figure 9. —A. *Adiantopsis reesii* (E. L. Ekman 9987, F). Scale bar = 3 cm. —B. Ultimate divisions of *A. reesii* with toothed apices. Scale bar = 0.25 cm. —C. *Adiantopsis rupicola* (Britton 7497 et al., US). Scale bar = 3 cm. —D. Ultimate divisions of *A. rupicola*. Scale bar = 0.75 cm.

color and texture; *rachis* 1.1–1.5 mm basal diam.; *carinae* golden, grading into lamina; *scales* appressed to patent, narrowly rhombic to lanceolate, 0.70–1.60 mm long, 0.05–0.19 mm wide, bases acute, apices acute. *Pinnae* ascending, 23–55 pairs, alternate, slightly incurved in basal half of lamina, straight distally, narrowly triangular to linear, slightly inequilateral to equilateral, to 5.7–8.2 cm long, 1.8–3.7 cm wide, apices cuneate to acuminate. *Pinnules* ascending to slightly ascending, narrowly triangular to narrowly lanceate, to 1.2–2.3 cm long, 0.7–1.10 cm wide, basiscopic pinnules slightly larger than acroscopic pinnules, apices obtuse to acute. *Ultimate divisions* ascending, articulate, narrowly oblong, oblanceolate, to nearly flabellate, 3.4–9.1 mm long, 1.2–3.8 mm wide, bases cuneate, margins entire to crenulate proximally, crenulate distally, apices round, acuminate to acute; *stalks* persistent, not swollen at junction with laminar tissue, 0.3–0.6 mm long. *Veins* pseudodichotomous, anadromous, impressed to immersed in lamina, prominent. *Pseudoindusia* distinct, lunate to quadrangular, green to white proximally, hyaline distally, occasionally black maculate, 0.44–0.92 mm long, 0.30–0.44 mm wide, margin erose to entire. *Sporangia* subglobose, long stalked, arcus of 9–17(–23) indurated cells, these 21.19–48.90 μ m tall. *Spores* 64 per sporangium, tetrahedral-globose,

golden at maturity, white to pale yellow when immature, 30.97–44.83 μ m diam., echinate, echinae bases complete, laesura obscured by ornamentation. *Chromosome number* unknown.

Distribution and habitat. *Adiantopsis reesii* occurs on the islands of Hispaniola and Jamaica. It has been collected on shaded limestone cliffs and slopes, at up to 900 m altitude. Like many other *Adiantopsis* species, *A. reesii* is known from only a few collections and appears to be rare. However, the species is probably still extant, because it occurs in rural areas with little economic development. Additionally, recent ecotourism business in the Cockpit Country of Jamaica may protect its habitat from economic development.

Notes. *Adiantopsis reesii* is distinctive in its toothed ultimate division apices that distinguish it from other pinnate *Adiantopsis*. Further, the ultimate divisions of *A. reesii* are rather elongate compared to other pinnate taxa such as *A. rupicola*, *A. parvisegmenta*, and *A. vincentii*.

Adiantopsis reesii is a putative diploid, as evidenced by the sizes of its guard cells, spores, and indurated arcus cells. This species appears to be one diploid parent, along with *A. radiata*, of the putative tetraploid *A. pedata*. The distinctly toothed apices and ascending

ultimate divisions of *A. reesii* are evident in *A. pedata*. Future molecular research should examine this hypothesized relationship.

Selected specimens examined. HAITI. **Grand' Anse:** Massif de la Hotte, gr. Morne Rockhelois, Meragoaire, at Trou-Gorie, *E. L. Ekman* 9987 (BM, F [2], NY, UC, US); Massif de la Hotte, W group, Tiburon, Morne Sentier, *E. L. Ekman* 10608 (K, US); Massif de la Hotte, gr. M. Rockhelois, Meragoaire, *Ekman* 7965 (US).

JAMAICA. **Trelawny:** Cockpit Country ca. 5 mi. N of Quick Step, above Aberdeen P.O., *G. R. Proctor* 4090 (US). **Unknown Parish:** *R. V. Sherring* s.n. (BM).

8. *Adiantopsis rupicola* Maxon, Contr. U.S. Natl. Herb. 10: 485. 1908. TYPE: Cuba. Pinar del Rio, collected in mtns. near El Guama, crevices of partially shaded cliffs, limestone, rare, *W. Palmer* 242 & *J. H. Riley* (holotype, US!; isotypes, K!, MO!, US!). Figures 9C, D.

Rhizome ascending to decumbent, to 2.2 cm long, 0.6–1.2 cm diam.; *scales* bicolorous with a black to dark brown center and golden margins, acicular to linear, basifixed, 1.60–3.60 mm long, 0.30–0.36 mm wide, bases truncate, margins slightly repand, apices acute. *Fronds* strict, 23.5–50.2 cm long. *Stipes* atropurpureous to atrocastaneous, occasionally bicarinate, shorter than lamina, 4.0–17.5 cm long, 0.6–1.7 mm basal diam.; *carinae* when present, beginning in upper ¼ of the stipe and continuing into the rachis; *scales* extending 1.9–7.1 cm up the stipe, divergent, concolorous, tan, acicular to lanceate, pseudopeltate to basifixed, 1.00–6.64 mm long, 0.06–0.70 mm wide, bases biauriculate to truncate, margins slightly repand to entire, apices attenuate; *hairs* septate-capitate. *Laminae* tripinnate, narrowly triangular to lanceate, drying dull green to brown, 11.0–39.5 cm long, 4.2–17.5 cm wide, apices difform, attenuate; *laminar tissue* thin-spongiose to chartaceous, hydathodes marginal; *hairs* with basal cell elongate, clear or white, middle cell short, tan or clear, apical cell bulbous, clear, white, or golden; *stoma* complanate, guard cells 42.38–57.05 µm long. *Laminar axes* marcescent with costae curling acroscopically, atropurpureous to atrocastaneous, grading into lamina and taking its color and texture; *rachis* 0.6–1.5 mm basal diam.; *carinae* golden, grading into lamina; *scales* appressed to patent, narrowly lanceolate, 0.67–1.12 mm long, 0.08–0.16 mm wide, bases acute, apices attenuate. *Pinnae* ascending, 21–24 pairs, alternate, frequently incurved in basal half of lamina, straight distally, narrowly triangular, slightly inequilateral to equilateral, to 3.2–16.0 cm long, 0.9–5.5 cm wide, apices acute to attenuate. *Pinnules* patent to slightly ascending, narrowly triangular to linear, basal pinnules 0.7–3.9 cm long, 0.5–1.5 cm wide, basi-

scopic pinnules slightly larger than acroscopic pinnules, apices acute. *Ultimate divisions* slightly ascending to patent, articulate, oblong to trullate, 3.8–9.5 mm long, 2.0–5.5 mm wide, bases acute to cuneate, frequently uniauriculate acroscopically, margins entire, apices acute to round; *stalks* persistent, not swollen at junction with laminar tissue, 0.1–0.5 mm long. *Veins* pseudodichotomous, anadromous, immersed in lamina, occult to obscure. *Pseudoindusia* distinct, lunate to quadrangular, green to white proximally, hyaline distally, occasionally black maculate, 0.42–0.70 mm long, 0.30–0.40 mm wide, margin erose to slightly erose. *Sporangia* subglobose, long stalked, arcus of 12–21 indurated cells, these 32.6–42.38 µm tall. *Spores* 64 per sporangium, tetrahedral-globose, golden at maturity, white to pale yellow when immature, 34.23–40.75 µm diam., echinate, echinae bases complete, laesura obscured by ornamentation. *Chromosome number* unknown.

Distribution and habitat. *Adiantopsis rupicola* is endemic to the province of Pinar del Río, Cuba. The species has been collected on shaded, rocky limestone slopes or cliffs. Similar to other *Adiantopsis* taxa, *A. rupicola* is known from few collections. Although there are no recent collections of *A. rupicola*, it probably still occurs in Pinar del Río and is likely protected within the boundaries of Valle de Viñales National Park.

Notes. *Adiantopsis rupicola* may be confused with *A. vincentii*. The carinae of *A. rupicola* begin in the apical quarter of the stipes, whereas the carinae of *A. vincentii* begin in the basal half of the stipes. Also, *A. rupicola* has a mode of 16 indurated arcus cells, whereas *A. vincentii* has a mode of 14. The generally smaller, obovate to oblong ultimate divisions and lanceate to lanceolate lamina of *A. vincentii* also distinguish it from *A. rupicola*, which has generally larger ultimate divisions that are trullate to oblong and a narrowly triangular to lanceate lamina. Additionally, *A. vincentii* appears to be hemi-dimorphic with smaller sterile fronds, whereas *A. rupicola* shows no signs of dimorphism.

Guard cell, spore, and indurated arcus cell sizes place *Adiantopsis rupicola* in a group of putative diploid species. This species may be a parent, along with *A. radiata*, of some component of the putative tetraploid *A. pentagona*. The overall ultimate division shape of *A. pentagona* resembles the generally trullate divisions of *A. rupicola* more than those of any other extant, pinnate species. Additionally, having the carinae begin in the upper half of the stipes is unique to these two species. However, *A. rupicola* may not be the parent of all elements of *A. pentagona*. Some specimens of *A. pentagona* have

a tendency toward relatively larger and slightly more compound laminae and smaller ultimate divisions, suggesting an *A. parvisegmenta* parentage for these collections.

Adiantopsis rupicola is frequently spelled incorrectly as *A. rupicola*. Tryon and Tryon (1982) consistently use this incorrect spelling, and some specimens are determined with it. However, Maxon (1908) published the species as *A. rupicola*, and on subsequent determinations used that spelling. Therefore, *rupicola* does not appear to be an orthographic error and should be used.

Selected specimens examined. CUBA. **Pinar del Río:** Trail from Buenaventura to San Juan De Guacamalla, *P. Wilson 9349* (NY [2], US); Vedado, Habana, Las Pozas, N slopes of Pan de Guajabon, *Bro. Alain 2416* (US); Valle del Ruisenor, near Vinales, *G. R. Proctor 16363* (GH [2]); Banos San Vicente, *V. L. Britton 7497*, *E. G. Britton*, *C. S. Gager* (NY, US); El Valle de Ancon, near San Vicente, *C. V. Morton 9791* (DUKE, US); Sierra Guacamayas, Mogoc de la Baliza, on mtn. top, *E. L. Ekman 17986* (US); Limestone hills between Rio Cuaguateje and the Sierra Guane, *J. A. Shafer 10453* (GH, NY, US); On limestone rock, N foot of Costanera de San Vicente, *Bro. Leon 14352* (NY).

9. *Adiantopsis vincentii* M. S. Barker & Hickey, sp. nov. TYPE: Cuba, Las Villas, Las Vegas de Mataguá, Trinidad Mtns., Feb. 22, 1956, *C. V. Morton 10819* (holotype, US!; isotype, DUKE!). Figure 10.

Laminae tripinnatae; axes marcescentes. Ab *A. parvisegmenta* segmentis ultimis fertilis planis, textura papyracea, ab *A. reesii* segmentis ultimis praebentibus apices integros, rhachidibus 0.6–1.2 mm diametro ad basim, et ab *A. rupicola* segmentis ultimis obovatis vel oblongis, laminis lanceatis vel lanceolatis, arcu e cellulis induratis 14 (modus) composito differt.

Rhizome erect to repent, to 2.7 cm long, 0.5–1.5 cm diam.; *scales* bicolorous with a black to dark brown center and golden margins, narrowly lanceate to acicular, basifixed, 2.60–5.68 mm long, 0.20–0.44 mm wide, bases truncate, margins entire to slightly repand, apices attenuate to cuneate. *Fronde* strict, 13.2–36.5 cm long. *Stipes* atropurpureous to atrocastaneous, always bicarinate adaxially, shorter than lamina, 2.9–13.8 cm long, 0.7–1.8 mm basal diam.; *carinae* beginning in basal ½ of stipe and continuing into rachis; *scales* extending 1.5–[2.13]–3.4 cm up the stipe, divergent, concolorous, tan, narrowly lanceate to acicular, pseudopeltate, 0.70–2.80 mm long, 0.06–0.46 mm wide, bases biauriculate to truncate, margins slightly repand to entire, apices attenuate; *hairs* septate-capitate. *Laminae* tripinnate, lanceate to lanceolate, drying green to brown, 12.2–28.5 cm long, 4.2–10.5 cm wide, apices difform, attenuate; *laminar tissue* papyraceous, hy-

dathodes marginal; *hairs* with basal cell elongate, clear or white, middle cell short, tan or clear, apical cell bulbous, clear, white, or golden; *stoma* complanate, guard cells 40.75–53.79 µm long. *Laminar axes* marcescent with costae curling acroscopically, atropurpureous to atrocastaneous, grading into lamina and taking its color and texture; *rachis* 0.6–1.2 mm basal diam.; *carinae* golden, grading into lamina; *scales* patent to appressed, linear, biseriate, 0.62–1.24 mm long, 0.02–0.04 mm wide, bases cuneate to truncate, apices attenuate. *Pinnae* ascending to patent, 23–32 pairs, alternate to sub-opposite, frequently incurved in basal half of lamina, straight distally, narrowly triangular to linear, slightly inequilateral, to 2.3–7.8 cm long, 0.7–1.8 cm wide, apices attenuate. *Pinnules* patent to slightly ascending, narrowly triangular to linear, basal pinnules 0.6–1.7 cm long, 0.3–1.0 cm wide, basiscopic pinnules slightly larger than acroscopic pinnules, apices cuneate to acute. *Ultimate divisions* patent to slightly ascending, articulate, obovate, oblong to elliptic, 2.7–6.0 mm long, 1.7–3.6 mm wide, bases cuneate, margins entire, apices round to acute; *stalks* persistent, not swollen at junction with laminar tissue, 0.1–0.5 mm long. *Veins* pseudodichotomous, anadromous, immersed in lamina, obscure to occult. *Pseudoindusia*, distinct, lunate to quadrangular, green to white proximally, hyaline distally, occasionally black maculate, 0.46–0.70 mm long, 0.40–0.50 mm wide, margin slightly crose to entire. *Sporangia* subglobose, long stalked, arcus of 12–16 indurated cells, these 32.60–52.16 µm tall. *Spores* 64 per sporangium, tetrahedral-globose, golden at maturity, white to pale yellow when immature, 32.60–44.01 µm diam., echinate, echinae bases complete, laesura obscured by ornamentation. *Chromosome number* unknown.

Distribution and habitat. *Adiantopsis vincentii* is a rare endemic in the Escambray Mountains of Cienfuegos, Sancti Spiritus, and Villa Clara Provinces, Cuba.

Notes. *Adiantopsis vincentii* is most likely to be confused with either *A. rupicola* or *A. parvisegmenta*. The generally smaller, obovate to oblong ultimate divisions and lanceate to lanceolate lamina of *A. vincentii* distinguish it from *A. rupicola*, which has generally larger ultimate divisions that are trullate to oblong and a narrowly triangular to lanceate lamina. *Adiantopsis vincentii* may be distinguished from *A. parvisegmenta* by three characters. The lamina of *A. vincentii* is papyraceous whereas the lamina of *A. parvisegmenta* is spongiose. *Adiantopsis vincentii* is tripinnate with a generally narrower lamina than the quadripinnate and broader lamina of *A. parvisegmenta*. Also, the fertile divisions of *A. vincentii* are



Figure 10. —A. *Adiantopsis vincentii* (C. V. Morton 10389, US). Scale bar = 3 cm. —B. Ultimate divisions of *A. vincentii*. Scale bar = 0.5 cm.

more or less flat, whereas the fertile divisions of *A. parvisegmenta* are strongly revolute.

Based on the sizes of guard cells, spores, and indurated arcus cells, *Adiantopsis vincentii* is placed with a putative diploid group of species. *Adiantopsis vincentii* is also the only hemi-dimorphic Caribbean *Adiantopsis*. On herbarium specimens with large rhizomes, and thus presumed to be mature plants, the fertility of the fronds is strongly correlated with frond size. The smallest fronds are consistently sterile, with a gradual increase in the number of sori and sporangia on progressively larger fronds. This pattern is not evident on specimens of other *Adiantopsis* taxa, and may serve as a useful character for recognizing the species if it can be confirmed to be unique.

Presently, *Adiantopsis vincentii* is not convincingly implicated in any patterns of reticulate evolution in *Adiantopsis*. However, it is possible that some elements of *A. pentagona* may have an *A. vincentii* parentage although no explicit hypothesis is presented. Future molecular studies should include *A. vincentii*, because the range of ultimate division variation in *A. pentagona* includes the character states that would likely be inherited from an *A. vincentii* parent.

Adiantopsis vincentii is named in honor of Michael A. Vincent, curator of the Willard Sherman Turrell Herbarium (MU) at Miami University, Oxford, Ohio. Dr. Vincent has continued to expand the collection at MU and has raised the Institution's standing in the world of botany through his activities as curator. Further, he has spent a significant amount of time dealing with research loans, and through these activities facilitates the research of many at Miami University.

Paratypes. CUBA. **Las Villas:** Trinidad Mtns., San Blas-Buenos Aires, *R. A. Howard* 6542 (GH, MO, NY [2]); Trinidad Mtns., Buenos Aires, *C. V. Morton* 10389 (US); Las Vegas de Matagua, Trinidad Mtns., *C. V. Morton* 10544 (US). **Unknown Province:** Cuba, *Eggers* 5399 (F).

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